HIERARCHICAL CONTROL OF CORAL REEF ECOSYSTEMS

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL OF THE
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Abstract of Dissertation Presented to the Graduate School of the
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Patterns of hierarchy and control were studied in coral reefs of
East Africa with field experiments, simulation models, and energy
analysis. The affects of reef control by the larger fishes and
calcareous structures were determined by comparing overfished
reefs with reefs protected from fishing. Reefs without normal fish
populations had surges of urchin population growth, more
competition, destructive erosion of calcareous reef structure, and loss
of diversity. Predators controlled many population and inter-
relationships. In particular, triggerfish regulated sea urchin
populations which indirectly controlled their grazing and over-

grazing of corals and algae. Unfished reefs, which had a high density of triggerfish, had low sea urchin densities ($<1/m^2$), high herbivorous fish abundance, high reef accretion rates and reef topographic complexity. Fished reefs, with fewer triggerfish, were dominated by herbivorous sea urchins ($5\text{-}20/m^2$) which eroded reefs and reduced coral reef complexity. Sea urchins competitively excluded herbivorous fish by reducing the abundance of algae below levels necessary to maintain herbivorous fish. The diversity of the sea urchin guild (about 10 species) was affected by triggerfish through preferential predation on the dominant urchin *Echinometra mathaei*.

Simulation models developed from eclectic coral reef data sources produced similar results to those found in field studies. Model results suggest that the intensity of fishing and the removal of high-level consumers effects unfished components and processes. Model results suggest that the transition from a fish-dominated to sea urchin-dominated ecosystem is rapid: an example of multi-equilibria controlled by human fishing. Leaving predators of invertebrates (i.e. triggerfish) unfished results in the highest fisheries yields and most intense fishing.

By using the emergy concept (spelled with an "m"), several kinds of energy that contribute to the reef ecosystem were expressed on a comparable basis in equivalent units of one kind of energy (solar emjoules/yr). Total annual emergy indicated that wave energy was the largest component. Evaluating the position of main reef components in the energy hierarchy using transformities (emergy per unit energy) indicated that fish and reef structure were highest in the energy hierarchy.

INTRODUCTION

Ecosystems are physical, chemical and biological systems that are maintained far from thermodynamic equilibrium. Consequently, the role of producers and consumers and the design of ecosystem structure that maintains their stability and production away from thermodynamic equilibrium remains a central focus of ecosystem science. Coral reefs are among the most complex ecosystems and are among those with the greatest diversity and abundance of consumer organisms. The role of consumers in the maintenance of ecosystem structure and processes may be important but has been poorly studied. This dissertation explores the factors that control East African coral reef community structure, diversity and some ecological processes through field studies, experimentation and simulation models. Specifically, the study focuses on reef building corals, algae, sea urchins, herbivorous fish, and piscivorous fish (Fig. 1, Odum 1983).

Questions of Hierarchical Control

Ecosystems are composed of interacting biological, chemical and physical components that are organized into interacting webs (Pimm

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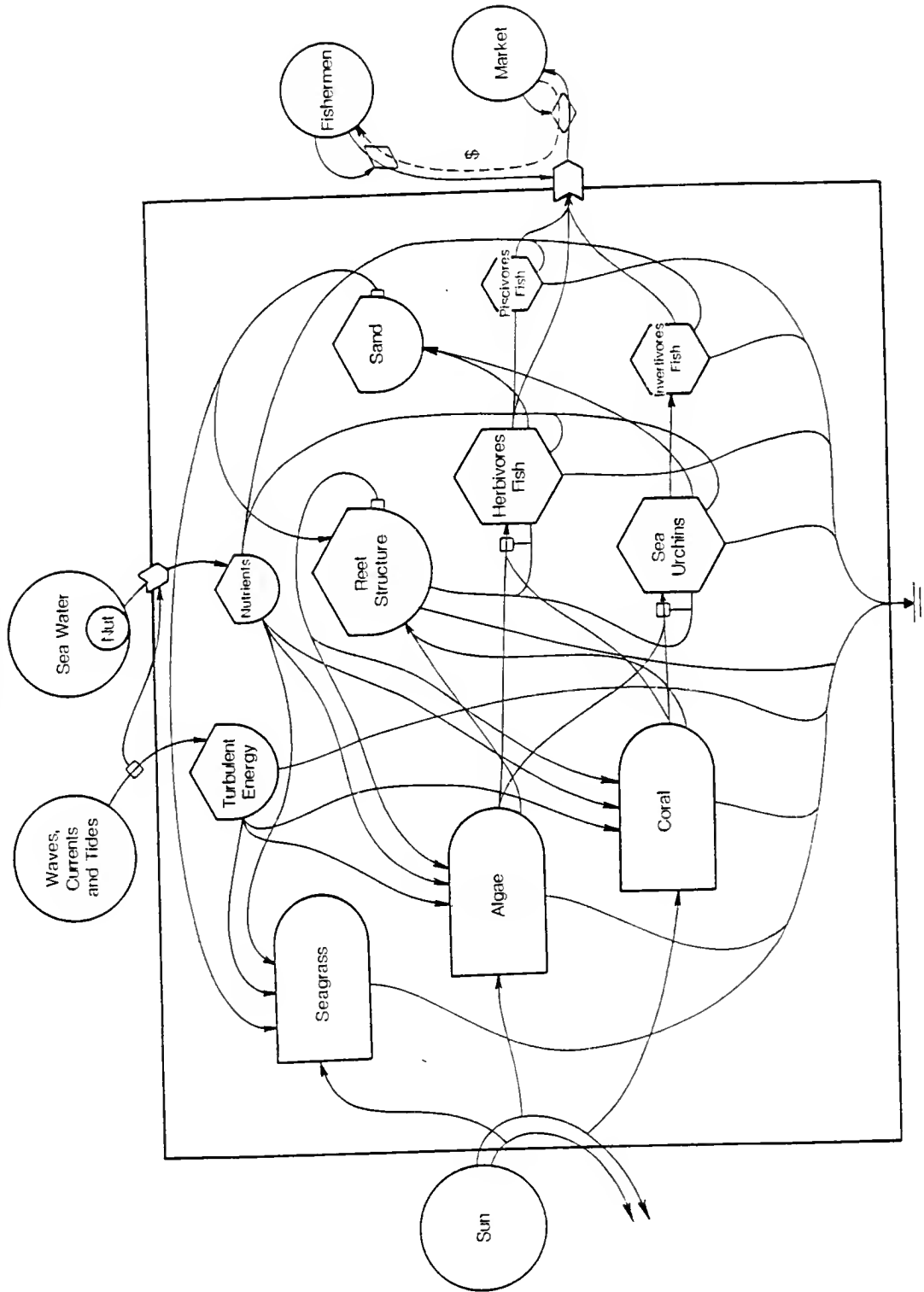
Fig. 1. Overview energy-circuit diagram of coral reef and coral reef fisheries.

1982, Odum 1983). Energy and nutrients transformed or taken up at the base of the food web can often follow multiple pathways before being recycled or lost from the ecosystem (Fig. 2). Energetic support for the food web is provided by the primary producers but energy may follow multiple pathways dependent on consumer choices. On the long term, choices may be evolutionarily determined by predator-prey interactions (Janzen 1980). On the short term, choices may be more flexible and based on optimal foraging considerations (Schoener 1971).

As energy is transferred between trophic components the amount of energy decreases. Yet, energy embodied in each component increases with increasing trophic level (Fig. 2). Schoener (1989) evaluated food webs and found, on average, that each trophic "species" predator has 2 trophic "species" prey. Consequently, the number of embodied connections or pathways increases with increasing trophic position. The potential for control may increase with increasing trophic level due to the increase in embodied pathways and the greater choices and flexibility of top-level consumers. A hypothesis of ecosystem organization is that as energy embodied per trophic level or species increases so does the potential for control of the ecosystem (Odum 1983). Decisions about prey choice and consumer feedback at the top of the trophic pyramid can influence the abundance of specific organisms and interactions between and within trophic elements. These choices may have surprising outcomes due to the complexity of interactions beneath the trophic elements. Multiple pathways within ecosystems permit
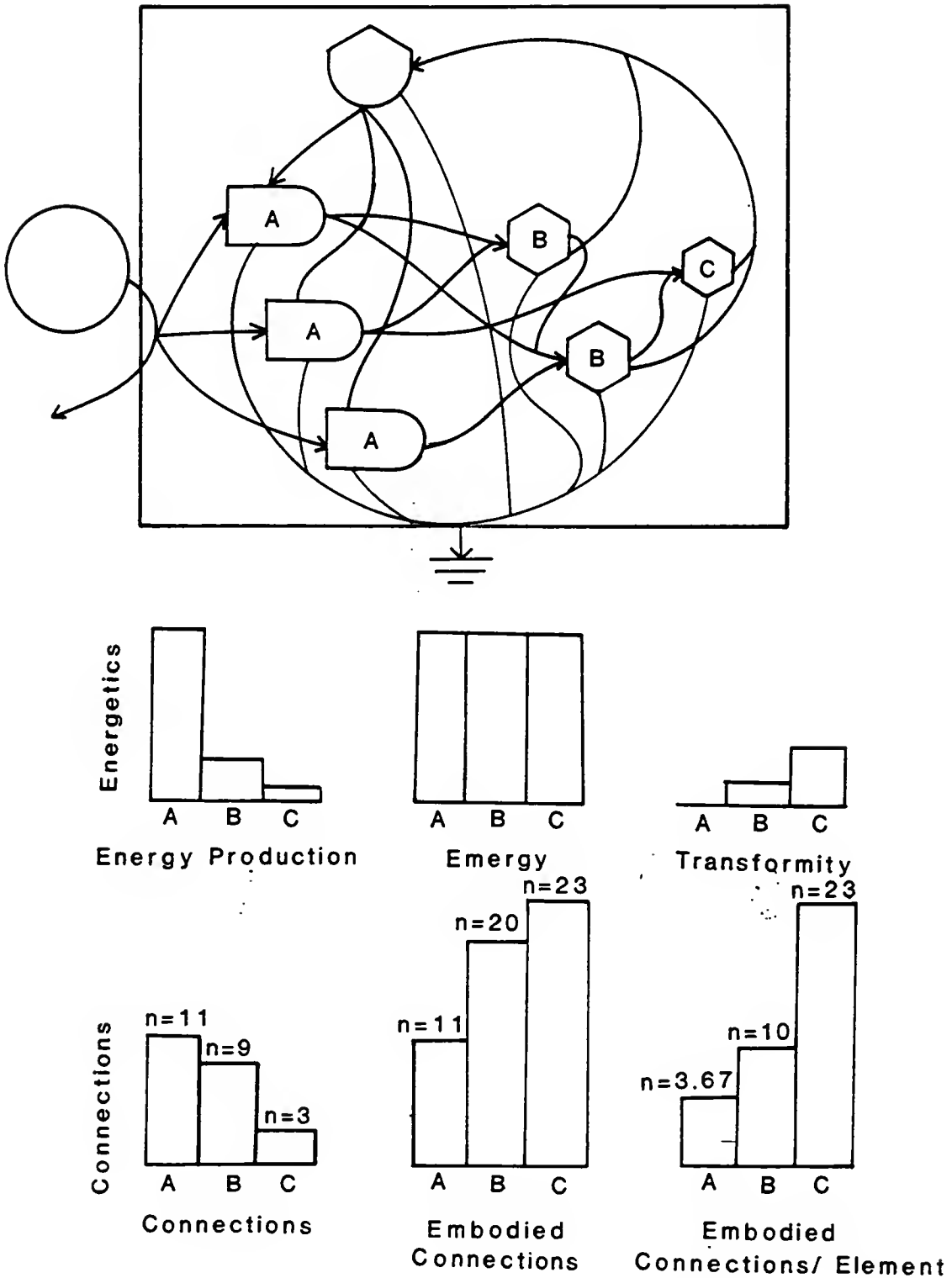
Fig. 2. Hypothetical food web with 3 trophic levels (A, B, C).
The energetics and connections (nonheatsink) for each level are
analized. Energetic histograms show the energy, embodied
energy and transformity (emergy/energy) of each component.
Connections shows total connections, embodied connections and
connections per element.

ecosystems to have multiple states dependent on control processes (Holling 1973).

Design of Self Organizing Systems

In ecology, as in the science of general systems, major unsettled questions concern the systems designs that emerge from the self organizational process. Answers to these questions about organization come from study of the parts, their inter-relationships, field experiments where manipulations result in changed relationships or through computer simulation experiments of different designs and intensity of interactions. Many of the controversies in ecology about population regulation and ecosystem design can be summarized by systems diagrams which avoid definitional or semantic arguments.

Figure 3 presents four possible designs of consumers and producers that may occur in ecosystems. The simplest and perhaps most frequently described interaction (i.e. Lotka-Volterra predator-prey interactions) is a consumer that simply removes a certain fraction of its prey (Fig 3a). Yet, consumers may have different effects on their producers that may feedback on production processes. Consumers may preferentially select different species, guilds or parts of an organism (i.e. leaves versus stems) which gives a competitive preference to unselected component (Fig. 3b). This relationship can be described as compensatory as it gives one component a competitive advantage over another which can
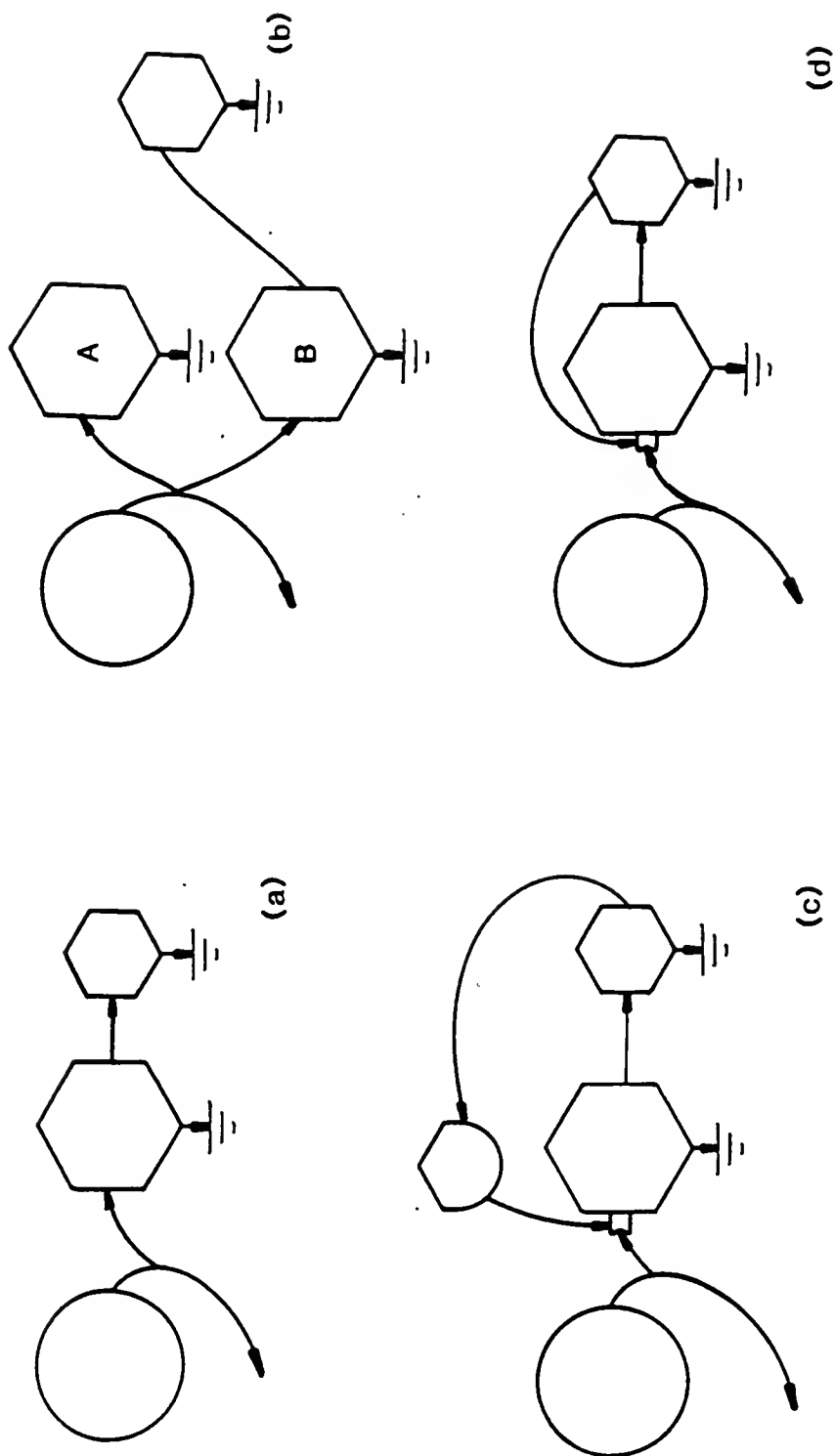
Fig. 3. Four possible designs of production between producers and consumers. (a) a simple drain from the producers (b) a selective choice by the consumer which gives one producer (A) a competitive advantage over the other (B), (c) a material recycle process and (d) a direct effect of the consumer on the production process.

compensate for its competitive inferiority in the absence of consumers. Additionally, consumers can affect production through mineral recycling (Fig. 3c) or through direct effects on producer production processes (Fig. 3d). All of these designs may result from self-organization but their relative importance requires further field studies of ecosystem design and experimentation.

Emergy, Transformity and Hierarchy

One method to describe the hierarchical structure of an ecosystem is by calculating the energy used in generating an ecosystem element. This measure has been given the name emergy which is a measure of the energy used to generate an element, usually expressed in emjoules (embodied joules). Transformity is the ratio of emergy divided by the actual energy of a component and is a measure of a component's hierarchical relationship with other elements. The higher the transformity the greater the energy used to generate the element and the higher the element in the hierarchy. Calculating the transformity of components allows one to determine the hierarchical structure of the ecosystem. As in Figure 1, diagrams are organized from left to right with low transformity elements on the left and high transformity elements on the right.

In order to obtain a broad overview of the physical forces and the hierarchical arrangement of the coral reef, an energy/emergy analysis was performed using data from the East African region (McClanahan 1988). The main energy flows in the coastal marine

environment: sunlight, wind, rain (physical), currents, tides and waves make the high concentration of reef organisms possible. Their actions support and effect circulation, photosynthesis, and calcium carbonate deposition. Adey (1987) has emphasized the importance and the synergistic effect of physical forces in maintaining high reef production in the low nutrient environment of coral reefs.

Community Structure and Theories of Diversity

Competition, Predation, and Disturbance

The causes of high species diversity in coral reefs has stimulated vigorous debate (Sale 1980). Early research suggested that coral reefs, over a long and stable evolutionary period, evolved resource partitioning mechanisms (Smith and Tyler 1972). Early studies implicated energy as an important determinant of diversity as high and stable energy inputs in coral reefs differentiated coral reefs from other less diverse ecosystems (Connell and Orias 1964) which may allow greater diversification and specialization of production tasks (Odum 1963). Subsequent work has challenged this view and suggested that high species diversity is maintained by frequent perturbations which keep species from monopolizing resources and causing competitive exclusion (Sale 1977, Connell 1978). Disillusionment with the competitive resource hypothesis resulted from the difficulty of measuring interspecific competition between closely related fish species (Sale 1980). If competition has

created observed species diversity it is difficult to measure at present. Connell (1980) suggested that utilizing the competitive resource partitioning hypothesis to explain observed patterns was to resurrect "the ghost of competition past." Yet, subsequent work in favor of a "nonequilibrium" view has not been rigorous and is largely based on observed hurricane induced mortality (Leviten and Kohn 1980), patterns of species richness in calm and disturbed habitats (Abele 1976) and turnover rates of fish populations (Talbot *et al.* 1978, Sale 1979). Consequently, factors contributing to coral reef species diversity are still open to debate.

Whereas competition has been difficult to measure in coral reefs (although, see Williams 1981, Hay and Taylor 1985, Robertson and Gaines 1986) , predation and herbivory are readily observed. Biomass and species composition of algae may be greatly affected by the abundance of herbivores (Hay *et al.* 1983, Hay 1984, Lewis 1985, Lewis 1986). Carnivore control of biomass and species composition has been shown for coral-fish and sea urchin-coral interactions (Neudecker 1979, Sammarco 1980, Carpenter 1981, Wellington 1982), coral-sea star interactions (Moran 1986), fish predation on sea urchins (McClanahan and Muthiga 1989) and on gastropods (McClanahan 1989). Predation may control coral reefs and indirectly regulate competition through keystone species (Paine 1966) or compensatory mortality interactions (Connell 1978). Shifts in species composition have the potential to influence many ecological processes such as productivity, nitrogen fixation and calcium carbonate deposition.

To determine the importance of biological control in maintaining coral reef species diversity, an intensive study was undertaken on three common sea urchins, *Diadema setosum, D. savignyi* and *Echinometra mathaei* that inhabit reef lagoons. McClanahan and Muthiga (1988) hypothesized that: 1) *E. mathaei* is the top competitor of this guild, 2) *E. mathaei* is the species most susceptible to predation, and 3) that the 3 species inhabit different microspatial locations in the reef that are maintained by differential predation on the three species. In the absence of predation the competitive dominant, *E. mathaei*, should undergo population increases resulting in the competitive exclusion of subordinate species.

Structural Complexity

The reef's topographic complexity.is a notable attribute of coral reefs that has been suggested to control the abundance and diversity of coral reef organisms. The combination of coral calcium carbonate deposition and physical and biological erosion create a sculptured and complex physical environment. Kohn (1967) suggested that reef complexity allowed for spatial resource partitioning of species which maintained species diversity. Subsequent work on fish also indicates that fish abundance and diversity appear to be affected by reef complexity (Luckhurst and Luckhurst 1978, Bell and Galzin 1984). Reef complexity could potentially allow spatial resource partitioning based on competitive interactions or may simply provide predator

refuge which allows more individuals and species to persist in the face of intense predation. In order to maintain reef complexity over the long term, calcium carbonate accretion must exceed erosion.

In this study, rates of bioerosion and the topographic complexity of reef lagoons were measured in reefs with various sea urchin densities to test the hypotheses that 1) individual sea urchin reef erosion rates should increase with increasing sea urchin density and 2) that reef complexity should decrease with increasing sea urchin density due to increased reef erosion by sea urchins.

Population Regulation

Population regulation can affect the maintenance of diversity by the impact of one population on another. In addition, grazing intensity and prey selection may affect ecological processes such as productivity and ecosystem structure (i.e. the calcium carbonate storage of coral reefs). Population regulation of coral reef organisms can occur due to low levels of reproduction, starvation or predation during planktonic stages (Doherty 1983), benthic predators (Wellington 1982, Shulman 1985, McClanahan 1989, McClanahan and Muthiga 1989), intra- and interspecific competition (Robertson and Gaines 1986, McClanahan and Shafir 1990), disease (Lessios et al. 1984) or environmental factors such as intense storms (Connell 1978, Leviten and Kohn, 1980). The model of Shulman and Ogden (1987) indicates that pre-settlement mortality in benthic habitats is an important population control only if post-settlement mortality is low.

Yet, what regulates coral reef organisms when predator densities and postsettlement mortality are low and settlement is high? Do coral reef organisms have density-dependent population regulation mechanisms that result in a balance between populations and resources?

Recent marine benthic population work has suggested that many species are "recruitment limited" (Doherty 1983, Roughgarden et al. 1988, Hughes 1990, Karlson and Levitan 1990); which means that populations are 1) not in equilibrium with their resources (Sale et al. 1984), or 2) that density-dependent mortality does not occur (Doherty 1983). In contrast, more traditional population models suggest that density-dependent mortality due to aggressive behavior, intra-specific competition, and subsequent density-dependent mortality can regulate populations (Pearl and Parker 1922, Wynne-Edwards 1965). This mechanism has been suggested for birds (Lack 1966, Klomp 1972) and other organisms (Wynne-Edwards 1965, Bustard 1970, Lamincki 1988).

Experimental density manipulations of adult coral reef organisms (Sale 1976, Williams 1978) have resulted in population changes. But, Doherty (1983) suggests that population density changes represent a redistribution of individuals, not mortality or population regulation at the larger scale, which requires experimentation focusing on density-dependent juvenile-adult interactions. Work on juvenile-adult interactions suggests species-specific density-dependent interactions as experimental results have shown both positive, negative and no interactions between juveniles and adults (Doherty 1983, Shulman et al. 1983, Sweatman 1985,

Jones 1987). Research on benthic marine invertebrates also suggests that recruitment may or may not limit populations depending on the abundance of larval settlement (Connell 1985, Roughgarden *et al.* 1988). Levitan (1989) found that size, growth and species biomass of a common Caribbean sea urchin *Diadema antillarum* was affected by the abundance of food. Population densities of *D. antillarum* may be regulated by periodic diseases (Lessios *et al.* 1984), which may or may not be density dependent, rather than strictly density-dependent mortality (Karlson and Levitan 1990) due to predation or competition.

As predation intensity is reduced, does intra- and interspecific competition become progressively more important in regulating populations? Are the competitively subordinate species populations regulated by competitively dominant populations? What will control competitively dominant species populations when predator populations are absent or reduced? *Echinometra* differs from *Diadema* as it variably exhibits inter- and intraspecific aggressive behavior and has the ability to force other organisms out of its burrows (Grunbaum *et al.* 1978, Tsuchiya and Nishihara 1985, Neill 1988). The intraspecific aggressive behavior of *E. mathaei* may regulate its population densities below the level at which food resources are limiting.

A number of possible population and biomass regulation mechanisms are plausible. Perhaps the aggressive behavior of *E. mathaei* maintains a constant population density through increased predation or food limitations on recruits, or perhaps population density increases in proportion to planktonic settlement such that

food eventually limits individual growth. This would suggest that biomass is regulated by energetic limitations rather than density-dependent population control.

In order to test these hypotheses I performed a series of measurements and experiments to determine the relative importance of density-dependent population regulation and food resource limitations. A series of short-term experiments that added or reduced populations were performed on the reef to determine 1) the ability for intraspecific behavior to regulate localized densities and behavior, and 2) the relative rates of predation on recruits compared to established individuals. Behavioral studies were undertaken to determine the relationship between population density and the frequency of aggressive behavior. Additionally, long-term population and recruitment patterns were measured over a four-year period.

Reduced food availability and competition for food should result in feeding adaptations and changes in body condition. Therefore, feeding and gut evacuation experiments were undertaken to determine if consumption rates of organic and mineral (calcium carbonate) matter were density-dependent. Measurements on respiration, gonad, body size and mouthpart size were made to determine the effects of body size and population density on individual morphology and physiology.

Role of Fishing

Despite the importance of coral reef fish as food in many tropical countries, there are few studies of coral reef fisheries. The complexity of coral reefs does not allow for simple fishing and harvesting schemes and as a result most coral reef fisheries are dominated by small-scale enterprises without research budgets. Additionally, the diversity of the coral reef fish assemblage has not attracted traditional fisheries studies based on single-species models. Finally, the incidence of toxic fish (i.e. ciguatera) makes fishing enterprises vulnerable to legal action. This discourages large-scale organizations that are capable of research.

Research suggests that the abundance of preferred game fish and particularly larger fish may be absent on fished reefs (Stevenson and Marshall 1974, Bohnsack 1982, Goeden 1982). Additionally, catch rates may decline (Munro 1983, Koslow *et al.* 1988), and shifts in species composition may occur (Koslow *et al.* 1988). Koslow *et al.* (1988) suggest that the complexity of coral reef fisheries may make them less stable and more vulnerable to overfishing. Sea urchin (Hay 1984, Hay and Taylor 1985, McClanahan and Muthiga 1989) and gastropod (McClanahan 1989) population densities may increase in fished reefs due to predator and competitor reductions. Mass mortality of *D. antillarum* in the Caribbean resulted in population increases of herbivorous finfish (i.e. parrot and surgeonfish) in areas previously dominated by sea urchins (Morrison 1988, Carpenter 1990). This suggests that sea urchins compete with herbivorous fish for algal food resources.

The following hypotheses about fishing are tested in this dissertation: 1) fishing increases sea urchin population density through a reduction in predators and competitors, 2) sea urchin population increases result in reduced herbivorous fish abundance beyond that which is attributable to fishing alone and 3) bioerosion is greater and reef accretion is lower in fished than unfished reefs

Modelling

To further understand coral reef processes, and to develop a fisheries management tool, simulation models were developed. Prior to the development of a coral reef fisheries model, which would attempt to describe the behavior of the coral reef under different fishing regimes, some simpler models of predation and competition were developed to determine the effect of different configurations and coefficients on the outcome of proposed interactions. Most models were simple predator-prey or competition models and were simplifications of the more complex coral reef model.

Models simulated included 1) the effects of a population's consumption and turnover rates on biomass, and subsequent yields to the next higher trophic level, 2) the effects of a population's lower food resource limit on the population's biomass 3) the effects of population turnover and consumption rates on competitive ability, and 4) the effects of harvesting on competitive ability. Each of these models helped in calibrating the larger model, and for understanding

dynamics of competition and predation and the impacts of fishing on these dynamics.

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The Coral Reef Environment

Coral reefs are major marine ecosystems of tropical latitudes. They harbor one of the world's most diverse species assemblages (Anderson *et al.* 1981), have among the highest productivities of either domestic or pristine ecosystems (Larkum 1983), fix significant quantities of nitrogen (Wilkinson *et al.* 1984), deposit 50% of the ocean's calcium carbonate and associated carbon dioxide (Smith 1978) and contribute 10% of the world's fisheries production (Smith 1978). Coral reefs are frequently located in near-shore environments between the $20^{o}C$ isotherms in regions without upwelling and large river discharges. Water temperatures are warm, water clarity is high and light penetrates to the benthos where most (> 95%) productivity occurs (Larkum 1983). Physical factors such as waves, currents, hurricanes, tidal range and temperature fluctuations are variable among and within regions and sites.

Reefs are frequently divided into three zones; the reef crest (or edge), the reef flat, and the reef lagoon (Fig. 4). The reef crest is the most seaward location and is exposed to the full force of waves, currents and hurricanes. Reef flats are frequently exposed to lesser extremes of waves and currents but are often exposed to air depending on their height and the region's tidal range. Reef lagoons are largely protected from physical forces, but they may experience
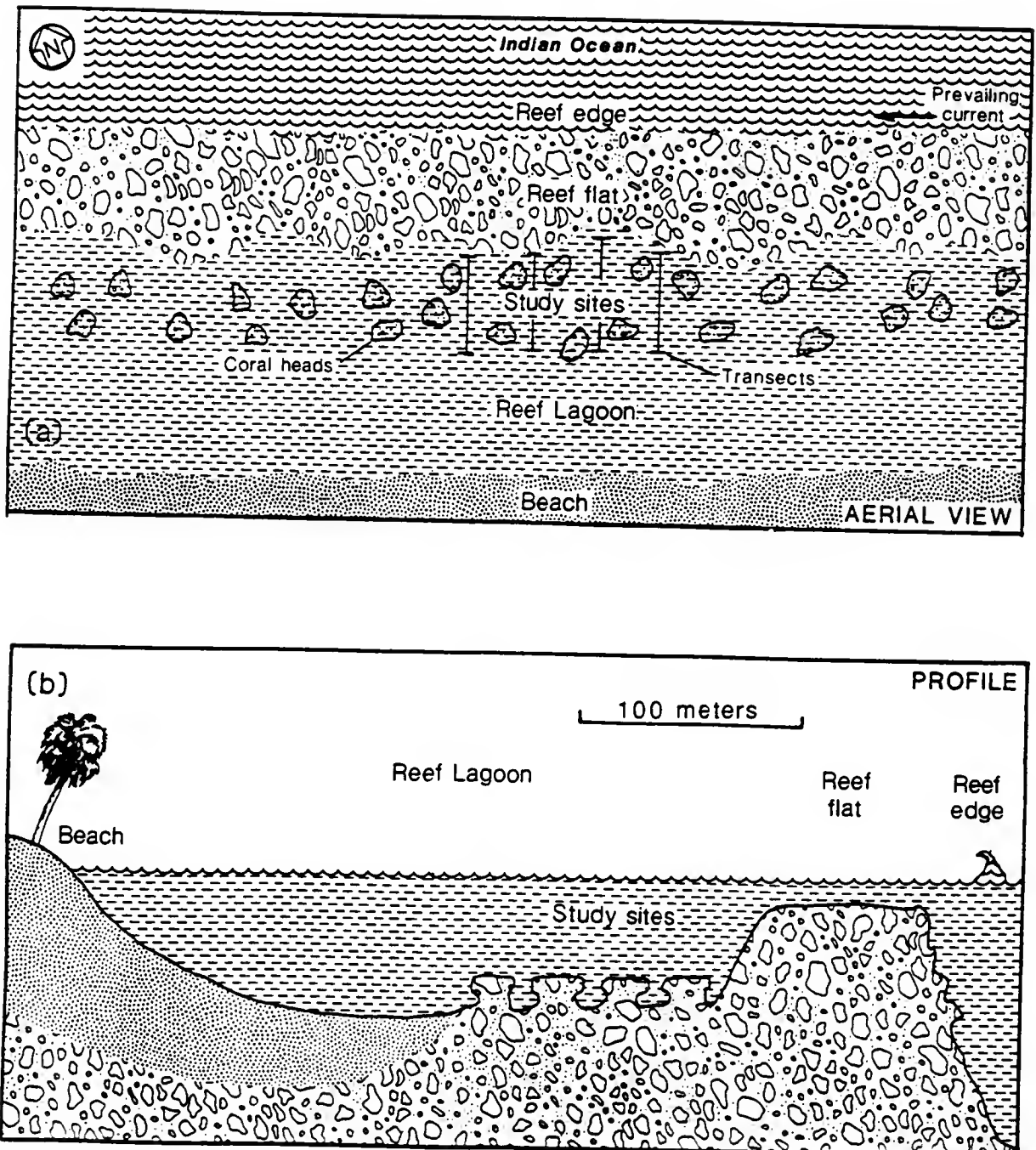
Fig. 4. Aerial (a) and profile (b) view of a typical Kenyan fringing reef, study sites and transect placement.

temperature and salinity changes if isolated from the ocean during low tides. Kinsey (1977) suggests that reduced water movements in reef lagoons reduces productivity and the rate of calcium carbonate deposition. Reduced impacts of physical forces in reef lagoons suggest that biological forces may be important controls. Research reported in this work was undertaken in reef lagoons.

Productivity

Coral reefs are highly productive and near the theoretical limits of primary production (Larkum 1983). Gross production varies from 2 to 12 $gC/m^2/day$ but averages around 8 $gC/m^2/day$ (Kinsey 1983, Larkum 1983). Most studies indicate P/R ratios near 1 although values both greater and less than 1 have been reported (Kinsey 1983). After coral and algal respiration, the majority (>90%) of net production is consumed by grazers (Carpenter 1986, Polunin 1988). The balance of gross production and total community respiration (P/R=1) may be changed by disturbances such as overfishing.

Measurements of nutrient contents in water flowing over coral reefs indicates no net uptake of phosphorus (Pilson and Betzer 1973), but net exports of nitrogen (Wilkinson *et al.* 1984). Nutrient enhancement studies indicate some production response to fertilization but only marginal increases. This suggests that despite the low nutrient concentrations of ambient waters, coral reefs are not

severely nutrient limited (Kinsey and Davies 1979, Williams and Carpenter 1988). Wilkinson *et al.* (1984) suggests that grazing fishes enhance nitrogen-fixing algae by selectively removing nonnitrogen-fixing forms. Grazing sea urchins have nitrogen-fixing gut symbionts that increase the nitrogen content of their feces and may, in turn, enhance primary production (Williams and Carpenter 1988). Hatcher (1983) suggests that reef productivity may be limited by grazers rather than any chemical or physical factor.

Calcium Carbonate Structure

Coral, coralline and calcareous algae, molluscs, sea urchins and other plants and animals remove calcium and carbonate ions from seawater and deposit calcium carbonate in their skeletons (Chalker 1983). Coral are the most important source of calcium carbonate deposition in most reefs. Average calcium carbonate deposition rates lie between 1.0 and 1.2 $kg/m^2/yr$ which translates into a vertical accretion rate of around 0.5 mm/yr (Smith 1983). This calcium carbonate forms the reef matrix which is bound together by algae, sponges, bryzoans and other organisms. The most speciose organismic assemblages are associated with hard substrate formed from calcium carbonate deposition and its subsequent binding.

Many organisms, both plant and animals, burrow and excavate the calcium carbonate substrate (Hutchings 1986). The most important bioeroders include parrotfish, sea urchins and in some locations sipunculan and polychaete worms (Ogden 1977, Hutchings 1986, Birkeland 1988). Comparisons between sea urchin and

parrotfish bioerosion indicate that sea urchins erode the substrate at rates 1 to 2 orders of magnitude greater than parrotfish (Ogden 1977, Birkeland 1988). Comparisons of sea urchin bioerosion range from 0.07 to 1.4 g/urchin/day. This large range may, in part, be due to differences in measurement techniques. The highest reported rates by Downing and El-Zahr (1987) used a superior method. At low latitudes, reefs with low sea urchin densities should have net accretion rates.

Kenyan Study Sites

The Kenyan coast south of Malindi (Fig. 5) is bordered by a nearly continuous fringing reef which lies between 100 m and 3 km offshore. Most areas have a shallow (0.5 to 5 m deep) reef lagoon that lies between the shore and the reef platform (Fig. 4). Lagoons are depositional environments dominated by sand and seagrass ecosystems, but also contain. hard substrate and coral outcrops. These coral outcrop areas harbor the greatest faunal diversity and field research was performed in these areas. Physical conditions in the reef lagoons are generally calm, particularly during low tides which makes field work relatively easy.

The Kenyan coastline has a variable human population density, but fishing is common in most locations. Two sections of the reef, Malindi and Watamu, have been designated as Marine National Parks (MNP) and have received complete protection since 1968. Fishing in reef lagoons includes beat-seining, spearfishing, traps and line
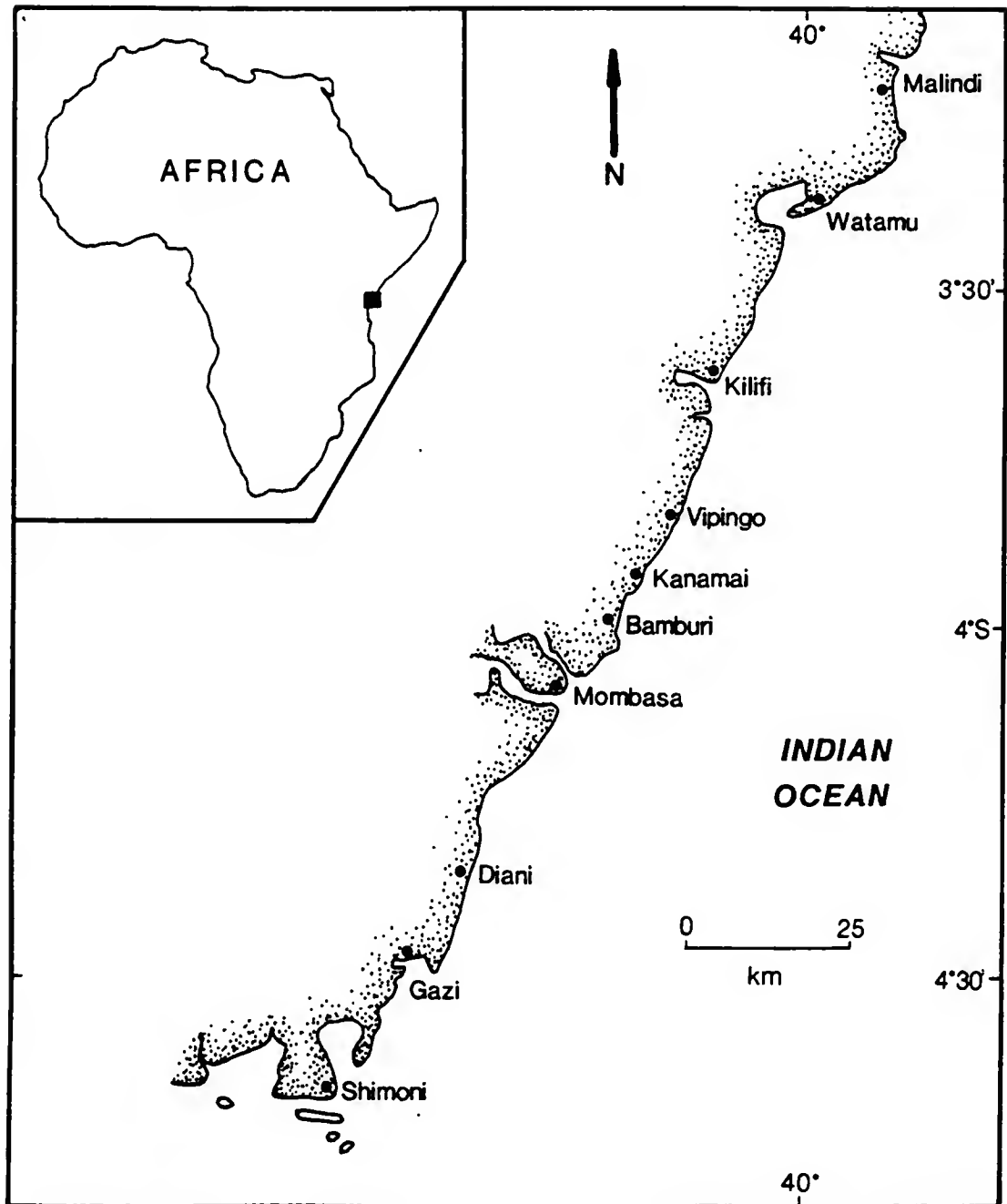
Fig. 5. Map of the southern Kenyan coast and study sites.

fishing. Fishing is largely part of a subsistence economy with fishermen selling part of their catch to neighbors and local markets. Many fishermen travel by foot to fishing locations, most fishermen lack boats and motorboats are very rare. For comparative purposes 2 protected reef sites (Malindi and Watamu) and 4 unprotected sites (Vipingo, Kanamai, Bamburi and Diani) were chosen. All research was done in the reef lagoons in areas dominated by coral outcrops, usually of the genera *Porites* or *Pavona*. Subsequent to this field work Bamburi was designated as a Marine National Park. All sites were chosen for their similarity in reef structure, in having shallow water (<2 m deep), calm conditions and hard substrate.

METHODS

Plan of Study

Research included field work along the Kenyan coast, spanning 3 years, in which basic field measurements of the coral reef community were made (i.e. substrate, fish, invertebrates) on 6 reefs which were *a priori* believed to represent different levels of fishing intensity. Field experiments were conducted to test hypotheses generated from field measurements and observations. During 2 years at the Center for Wetlands, University of Florida, an ecosystem model was developed based on field measurements and a literature review. Minimodels were developed to simulate the effects of different configurations of competition, predation, and control, where calibrations were from coral reef conditions. The effect of coefficient changes on yield rates to a high-level consumer was a major focus of simulation studies. Models were used to determine the effects of changing model coefficients and for calibration of the larger Coral Reef Fisheries Model. The Coral Reef Fisheries Model is an ecosystem model which was developed to test the impacts of fishing on major reef components and ecological processes.

Measurements of Community Structure

Within each of the six studied reef lagoons measurements were made on substrate cover and complexity, sea urchin species densities and fish population densities and sizes. Substrate cover and sea urchin population variables were measured in 1 to 3 randomly chosen locations per reef lagoon (a total of 14 sites). Each individual site covered a 30 m x 30 m area. Three parallel nylon lines separated by ten meters were established in each site (Fig. 4). The two ends and the middle of each line acted as foci for substrate and sea urchin density measurements. Consequently, each site consisted of 9 measurements except one site in Malindi and Bamburi where a single line was lost, thus reducing the sample size to 6.

Substrate Complexity

Substrate was sampled by a line transect method. A 1 cm by 10 m flexible nylon line was laid perpendicular to and bisecting the transect line. The distance covered by each category: hard coral, soft coral, algal turf (microscopic filamentous algae), calcareous algae (i.e. *Halimeda*), macroalgae (i.e., *Turbinaria, Padina* and *Sargassum*), coralline algae, coral sand, seagrass and sponge were measured to the nearest 1 cm and percent cover calculated.

Topographic complexity was calculated using the rugosity measurement (straight line distance/contour distance). The 10 m line was pressed against the substrate and allowed to follow the

bottom's contour for the 10 m distance. The straight-line distance which this 10 m line travelled was measured and rugosity was then calculated by dividing the straight line distance by the contour distance.

Sea Urchin Populations

Sea urchin population densities were sampled by circumscribing a nylon line of known length around the foci of the lines. Individuals encountered in the circle created by the circumscribed line were identified (Clark and Rowe 1971) and counted. Population densities varied by four orders of magnitude and therefore variable size quadrats of 2, 10 and 25 m^2 were used. Data were all adjusted to 10 m^2 areas (the area commonly reported in other coral reef sea urchin studies) for calculations of density, and diversity. Nonparametric rank order tests (i.e. Mann-Whitney U-test and Kruskal-Wallis test) statistics were used. These tests do not rely on measures of variance which are affected by the above normalization procedure (Sokal and Rolf 1981).

Sea Urchin Distributions

Within Kanamai and Vipingo a more extensive study was undertaken of the distribution and coexistence patterns between the 3 dominant sea urchin species *Echinometra mathaei, Diadema*

savignyi and *D. setosum*. Measurements included recruitment rates, distribution patterns and body morphology. Eight 100 m lines marked at 5 m intervals were laid parallel to shore at 50 m intervals and were visited and counted at low tides during the day. *D. setosum, D. savignyi* and *E. mathaei* were counted, and their frequency of occurrence in crevices, burrows, social groups and social group size were recorded in eighty 25 m^2 quadrats for *Diadema* and 10 m^2 quadrats for *E. mathaei*. Within each quadrat, body lengths, length of the longest primary spine, and the shortest length of the inhabited crevice, of up to 5 randomly selected individuals, were measured with calipers to the nearest half millimeter. Because *E. mathaei* has an elliptical shape, both the short and long axis were measured and the average used in calculations. Body lengths, weights and volumes were calculated. Body volume was calculated using the following equation for a half perfect sphere:

$$\text{body volume} = 2/3 \ \pi \ (\text{test length}/2 \ + \ \text{spine length})^3$$

Fish Populations

Fish populations were sampled by visual counts of individuals within a 5 m band between the swimmer and the line.along a 100 m line placed across the reef (Fig. 4). Three to five transects were made in each lagoon in the general vicinity of the transects made for sea urchin and substrate cover. The observer swam slowly (20 to 30 minutes/transect), counted all observed fish greater than 3 cm in length, assigned fish to 5 size categories (3 to 10 cm, 10 to 20 cm, 20

to 30 cm, 30 to 40 cm and > 40 cm), and 10 fish families (families listed in Result section) or an "others" category if the fish were not members of the preselected families. The 10 families were selected from all potential families because: 1) *a priori* they appeared to be the most common families based on density observations, 2) they were important algal grazer families, or 3) they were members of the sea-urchin predator guild (Randall 1967). Coral outcrops encountered in transects were circumnavigated in order to count and identify fish otherwise hidden from view. No fish < 3 cm were counted in order to reduce errors in density comparisons (Bellwood and Alcala 1988). Data were analyzed by comparing size-frequency distributions and densities of protected and unprotected reefs.

Community Structure Data Analysis

Densities, diversity, cluster analysis and Principal Component Analysis (PCA) were calculated on each set of population data. Diversity was calculated using a modification of the Simpson's Index (D) (Simpson 1949) with the following formula:

$$D = 1 - \Sigma \, (n_i/N_t)^2$$

where n_i is the number of individuals in a species and N_t the total number of individuals in all species combined. This index results in a number between 0 and 1, zero being the lowest and 1 the highest possible diversity. This index was chosen over other diversity

indices as it is easy to calculate, it gives a bounded range of diversity (0 to 1) and is less sensitive to error in small samples (Routeledge 1979).

Species-area curves were also calculated for sea urchins and the total number of species was estimated from these curves. Cluster analysis and PCA were performed to determine the similarity of the species assemblages in the different study sites. Cluster analysis used the Bray-Curtis (1957) measure of similarity and average between-group linkages (Ludwig and Reynolds 1988). Additionally, scatter-plots and correlations were performed between substrate, sea urchin and fish variables.

Field Experiments

Measurements of Predation

Relative rates of predation were determined for comparisons among the common species and among sites. Predation was measured in each reef lagoon by attaching threaded sea urchins to nylon transect lines. The tethering technique was introduced by (Ebert 1965) and developed more fully by McClanahan and Muthiga (1989). Sea urchins were pierced with a large hypodermic needle (60mm x 2 mm) and threaded with monofilament line. Urchins were then tethered to nylon transect line, visited daily and the urchins' presence or absence then recorded. McClanahan and Muthiga (1989) found that tagging induced less than 1% mortality; all other mortality

being attributable to predation. Since the technique restricts urchins outside burrows and affects their normal predator avoidance behavior, measures of predation have to be considered relative to the treatments.

Ten urchins were attached at 2 m intervals to each 30 m line for a total of 30 urchins per site. Sites were visited daily for three days, removal rates were recorded and the last day an urchin was alive was used as a measure of survival. Relative predation rates (P) were calculated with the following formula:

$$P = (t-x)/t$$

where x is the average survival in days and t is the total length of the experiment (3 days). This measure results in a value between 0 and 1 with 1 being the maximum rate of predation. A value of zero indicates that none of the urchins were eaten while a value of 1 indicates that all urchins were eaten.

Within Kanamai and Vipingo reef lagoons, a series of experiments were conducted to determine 1) differences in predation between the three dominant species (*E. mathaei, D. savignyi* and *D. setosum*), 2) the effect of burrow habitation on survival of *E. mathaei*, and 3) the effect of social behavior on survival of *Diadema*. To determine predation rates between species, threaded individuals were attached to nylon lines and species were alternated along the line. A total of 30 individuals per species were tied to lines in each reef and visited for 5 consecutive days.

The effect of burrow habitation on *E. mathaei* survival was determined by placing one group of tethered sea urchins in existing burrows and another group outside burrows. Both groups were fastened to the substrate and allowed 15 cm of free line. Sociality tests were made by tying groups of 2 to 5 individuals per species together on the same nylon line and allowing each individual 20 cm of line. Solitary individuals (15 to 29 individuals/reef) alternated with groups (24 to 42 individuals/reef).

Tests of Interspecific Competitive Behavior

The behavior of urchins that were competing for space was studied with field experiments on *E. mathaei*, *D. savignyi* and *D. setosum*. Experiments used an artificial shelter (crevice) constructed by bending a 50 x 16 cm rectangular piece of sheet metal into a semi-circle with a 15 cm radius and placing the convex site upward so that an opening occurred beneath and at both ends. Undersides of the sheet metal were painted with black polyurethane paint. Since the species are negatively phototaxic and positively thigmotaxic (Pearse and Arch 1969) I hypothesized that the species would compete for space beneath these shelters. Within Kanamai, 10 crevices were randomly placed throughout the reef lagoon. A species was chosen and placed within each of the shelters, allowed to acclimate for not less than 5 minutes at which time an additional animal was placed in 5 randomly selected shelters. Additional animals were either of the same or of different species. After 15

minutes, crevices were visited and the presence or absence of the initial and supplemental animals was recorded. The experiment was replicated at least three times for each possible inter- and intraspecific interaction. A G-test, which is an improvement on the Chi-squared test (Sokal and Rohlf 1981) , was used to test for differences between control and experimental crevices.

A series of additional experiments was undertaken to determine the more subtle interactions that occurred between the two *Diadema* species where crevice space was reduced. In order to test the effect of crevice size on competitive behavior, the above crevices were halved, experimental individuals were placed equidistant, but on opposite sides of the crevice entrances, tapped on the spines in the direction of the crevice and allowed to equilibrate their positions in the crevice for 3 minutes. After 3 minutes the amount of test hidden under the crevice for each individual was measured as well as each individual's test size. Individuals were considered to "win" competitions if they had a greater percentage of test beneath the crevice. Experiments included 1) interspecific competition between randomly chosen *D. savignyi* and *D. setosum*, 2) intraspecific competition between randomly selected *D. savignyi* , and 3) preferentially selected *D. savignyi* with larger test length and body sizes than *D. setosum*.

Intraspecific Competition and Population Regulation of *Echinometra mathaei*

In order to determine the population regulation ability of *E. mathaei*, a series of field experiments included short term density manipulation experiments, long term (about 4 years) population counts, and density-dependent recruitment, behavioral, morphological, and physiological studies. Studies were undertaken on three reef lagoons (Vipingo, Kanamai and Diani) that have different population densities and represent a continuum of inter-related factors of predation intensity, frequency of burrow habitation, and reef topographic complexity. Diani has the highest sea urchin density, followed by Kanamai and Vipingo. Vipingo and Kanamai lagoons were dominated by coral heads and *E. mathaei* most frequently inhabits crevices within these coral heads whereas Diani was dominated by coral rubble and *E. mathaei* are often found exposed (Muthiga and McClanahan 1987).

Density Manipulation Experiments

Population density experiments were done by adding and removing urchins from various reef lagoons and monitoring populations. Populations were monitored by counting individuals on the tops of small discrete *Porites* clusters. Within reefs at Kanamai and Vipingo the tops of circular *Porites* were randomly chosen and randomly allocated for either the addition of urchins, the removal of

urchins, or left as controls. Individual *E. mathaei* were counted, the short and long axes of the "coral head" were measured, circular area was estimated and population densities were calculated. *E. mathaei* were counted daily and followed until density was nearly constant (i.e. <2% change between consecutive days). The body size of *E. mathaei* (long + short axis/2) on haphazardly chosen individuals was measured before and at the end of experiments to look for body size changes resulting from the experimental manipulation. Within the reef at Diani, where coral heads were scarce, 1 m^2 areas were marked off and a population doubling experiment performed.

In a second experiment, individual urchins marked with acrylic paint (nail polish) were added to coral heads to compare population changes of new individuals and original inhabitants. Experimental individuals were collected, dried in the sun (5 to 20 minutes), given two coats of paint to their spines, dried and added to the experimental area, doubling the density of marked coral heads. On control heads, eight individuals were removed and replaced with marked individuals to maintain original densities. The number of tagged and untagged individuals in experimental and control categories were counted on consecutive days. Most (>90%) markings lasted 3 days before they began to wear off.

To determine the effect of predation on density changes that occurred during the first two experiments, experimental and control heads were chosen. Individuals were tagged on each head by piercing them with a hypodermic needle, threading them with monofilament and replacing them in their burrows (McClanahan and Muthiga 1989). On the following day seven more tagged individuals

were added to experimental heads along with untagged individuals until the density was doubled. Initial inhabitants (on control and experimental heads) and the additional individuals were strung together with nylon line, using differently colored lines to distinguish original urchins from those that were added. Approximately 0.5 m of line was allowed between individuals. Dead or missing individuals from each category were recorded daily for 3 days. Average survival rates were calculated and statistically compared. Attachment to lines may have decreased survival probability but mortality due to predation was distinguishable from other mortality by the animal's test condition. Predator-induced mortality and mortality attributable to other causes were distinguished in the analysis. Tethering techniques were used instead of caging because *E. mathaei* escapes from cages and Kenya's large tidal range (4m) damaged cages.

Behavioral Studies

Behavioral studies were undertaken on reefs at Diani and Vipingo to determine the frequency and types of aggressive behavior which might be attributable to different urchin population densities. A modification of the technique of Grunbaum *et al.* (1978) was used. Intruder individuals were placed at a host's burrow entrance and the result of the interaction recorded. Fights were followed for no more than 20 minutes. Two individuals remaining in the same burrow beyond 20 minutes were classified as coexistent, although they may

have been fighting beyond the time limit. This occurred infrequently (n=2) and only at the reef in Vipingo. Within the Diani reef, few individuals were found in burrows or crevices. Only individuals in crevices were used in experiments. Between-reef comparisons of behavioral categories were made with a G-test (Sokal and Rohlf 1981).

Starvation Experiments

To ascertain the response of individuals to starvation, 20 *E. mathaei* were placed in an aerated seawater aquarium. Seawater was replaced every 4 to 6 days and cabbage was supplied for food. Respiration was measured periodically over 9 days by oxygen uptake (Winkler titrations; Strickland and Parsons 1972) using rubber-sealed 1-liter mason jars for 1 hour (6 experimental jars and 1 control jar). After 9 days, the aquarium was divided, and half the individuals were starved. Periodic measurements of respiration were continued for 25 days. Cabbage was replaced daily and air-dry weights were measured before and after immersion. Additional control cabbage was placed apart from sea urchins. Daily consumption rates were calculated. At the end of the experiment, the individuals wet body and gonads were weighed. Respiration rates in the field, and gonad weights were measured for haphazardly-selected individuals from reefs at Diani and Vipingo for two different time periods (same method as above). To obtain averages for animals that might have differences on a lunar cycle

measurements were made at different stages of the moon. Field and laboratory respiration rates were measured at temperatures between 24 and 25°C. Test lengths (long+short axis/2), wet body weights, and lengths and weights of Aristotle lanterns (exposed tooth + lantern (jaw)) were measured. Gonad and lantern indices were calculated (lantern or gonad weight/body weight x 100). The dry weights of various body components and organic matter of cabbage were determined from drying at 60°C for 3 days. Ashed weights were measured after 3 hours of combustion at 550°C.

Population Counts

Periodic population density and test size measurements were made on Kanamai and Diani reefs between 1985 and 1988 (Muthiga and McClanahan 1987, McClanahan and Muthiga 1988). Wet weight was calculated from test length measurements with a length-weight correlation (Muthiga and McClanahan 1987). Dry organic matter weight was estimated using the above described combustion procedure data. In July 1988 the density of adult and recruits (test lengths < 1.5cm) were counted in haphazardly placed 1 m^2 quadrats on the three reefs. Recruits were small and hard to find and despite thorough searching, counts were undoubtedly underestimated although relative numbers are probably comparable. Within Diani, the cover of sand, hard substrate (dead coral), and seagrass cover was estimated for statistical comparison with 1985 data (Muthiga and McClanahan 1987) in 90 1 m^2 quadrats. Statistical comparisons

used running averages (i.e. $x = (x + x_{(d-1)} + x_{(d+1)})/3$; d=distance on transect) of the 90 quadrats. Running averages reduces the variance between quadrats and was able to detect within reef trends in density more accurately than data without running averages.

Measurements of Ecological Processes

Bioerosion

Substrate bioerosion by sea urchins may affect reef complexity. Previous researchers have measured bioerosion rates (reviewed by Ogden 1977, Hutching 1986, Birkeland 1988), but recently Downing and El-Zahr (1987) developed a new technique that was used on 3 Kenyan reefs (Vipingo, Kanamai and Diani) to determine rates of substrate bioerosion.

Sea urchins were removed from their burrows and placed in a predator exclusion cage (lifted above the substrate) from which 10 urchins were removed every 2 hours for eight hours. Removed sea urchins were sacrificed, their gut contents removed, dried and weighed on a triple beam balance. The gut content was then soaked in 1.13 N HCl to dissolve the calcium carbonate fraction, dried and weighed again. Plots of time since removal from the substrate and the remaining gut content give a rate of gut evacuation for both the organic and inorganic fractions of the gut. A daily substrate erosion rate was calculated assuming ingestion equals defecation. These

experiments were completed twice in Vipingo and Diani and 3 times in Kanamai.

Calcium Carbonate Deposition

Net rates of calcium carbonate deposition have been determined by an alkalinity depression technique (Smith 1978a) which measures carbonates deposited and/or dissolved from solution. A rough estimate of gross calcium carbonate deposition was made from coral cover measurements, known rates of vertical increase, and coral skeleton porosity. Gross calcium carbonate deposition was estimated with the following formula.

Deposition = Coral cover x linear growth rate x (1-porosity) x calcium carbonate density

The linear growth rate of massive heads (more than 80% of the coral forms found in the study sites) is about 1 cm/yr (McClanahan and Muthiga unpublished data). Aragonite has a density of 2.9 g/cm^3 and coral has an average porosity of 50% (Smith 1983). Therefore, from the above equation, multiplying coral cover by a factor of 14.5 will give a measure of gross calcium carbonate deposition in the units of kg/m^2/yr.

Models

Main features and mechanisms of the coral reef that were believed most important were combined using energy systems diagramming. Then, equations implied by the relationships and connections were written. To calibrate models quantitatively, a coefficient was calculated for each pathway and listed in the tables of coefficients. For calibration a value of each storage (state variable) and each pathway flow was estimated either from field measurements, a literature measurement from a similar system, or calculated by difference to make any unknown flows consistent with measured ones. The mathematical expression for each pathway was set equal to the pathway flow and then solved for the coefficient. For example, if

$$K1*A*B = 20 \text{ when the state variables } A=2 \text{ and } B=5$$

then

$$k1=20/(A*B) = 20/(2*5) = 2$$

My method of calculating coefficients assumed that each component had an upper maximum biomass (with predators absent), at which point gains and losses were equal. The component's (state variable) resource was then some fraction of its maximum. Consumption rates were usually estimated as some percentage of the maximum biomass as literature values are frequently reported this way. Turnover rates were assumed to be some daily percentage of maximum

biomass with gains equal to losses at this maximum level. After initial calibration, graphs of simulated variables were compared with real data. Models were frequently run by changing coefficients and then running the model to steady state for a variety of consumer levels. Steady state values were then plotted for different coefficients and consumer levels. More complete explanations of this methodology are given elsewhere (Odum 1983).

Energy and Emergy Analysis of a Coral Reef

Main energy flows used by an East African coral reef were estimated and compared in a table. Data on sunlight, rainfall and wave height on a monthly basis were previously summarized (McClanahan 1988). Tidal data were derived from tide table (Kenya Ports Authority 1988). Data were available on a monthly and annual basis.

Energy flows were also expressed in units of Emergy (spelled with an "m"), which compares each type of energy as equivalents of one energy type or as the energy of the one type required to produce the other type. Solar emergy is expressed in solar emjoules, the solar insolation energy required directly and indirectly to produce a flow or storage.

Solar transformity is the solar emergy per unit energy expressed in solar emjoules per Joule. Solar transformities used were previously calculated from the energy web of the biosphere

(Odum 1987). In the emergy analysis table solar emergy was calculated by multiplying each energy flow its solar transformity.

RESULTS

Coral Reef Emergy Analysis

Emergy Analysis

Results of calculating emergy use by a square meter of coral reef are given in Table 1. Although there is more solar energy received than other kinds of energy, on an Emergy basis the hydrodynamic contribution is much larger. Emergy calculations using presently known transformities indicate that the emergy comes from waves. Although there are large currents nearby (Table 1), current emergy absorbed in the ecosystem is less than the wave energy absorbed. Total solar emergy (item 6, Table 6) from independent sources was 2.82 E13 sej/m^2/year.

With hydrodynamic emergy in excess, direct solar energy may be limiting as high quality physical energy requires low quality solar matching emergy for its full effect. The seasonal pattern of emergy flows in waves and currents (Fig. 6). indicates that peak emergy occurs during the southeast monsoon when wind and wind-driven processes are prevalent.

An energy/emergy analysis of the reef's main biological components (Table 2) shows that algae have the highest production followed by coral, sea urchins, herbivorous fish, piscivores, and

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Table 1. Annual Emergy use by a square meter of coral reef community. Equations used in calculations given in Odum et al. (1987).

Note	Energy Type	Actual Energy Joules/m^2/yr	Transformity sej/j	Solar Emergy E+10sej/yr
1	Solar Energy	7.12E+09	1	.71
2	Waves absorbed	9.93E+08	25889	2570.00
3	Rain, physical	3.08E+04	15423	.05
4	Tides	1.07E+08	23564	252.00
5	Currents, kinetic	6.62E+08	5981	396.00
6	Total Emergy Used, item 2+4	1.43E+09		2822.00

1. Data from (McClanahan 1988) based on monthly averages from 1963 to 1980

   Average Insolation= 170 Kcal/cm^2/yr

   SI = 170 Kcal/cm^2/yr x 10000 cm^2/m^2 x 4186 Joules/Kcal

2. Data from McClanahan (1988) based on significant wave heights

   Average wave height= 1.39 m

   Average wave period= 8 seconds

   Average reef width= 100 m

   WE = 1/8 x 1.025 g/cm^3 x 980 cm/s x height^2 x 10000 cm^2/m^2 x 2.38E-11 erg/Kcal x 9.9 m/s x 0.125 s/wave x 3.15E+7 s/year / 100 m/reef

3. Kinetic energy of rainfall, data from McClanahan (1988) based on data from 1946 to 1980

   Average rainfall= 1.06E+03 mm/yr

   K.E.= rainfall mm/yr x 0.5 x 1 g/cm^3 x 762 cm/s x 2.38E-11 Kcal/erg x 4186 J/Kcal x 10000 m^2/cm^2

4. Tidal energy based on 1988 Kenyan tide tables (KPA 1988)

   Average tidal range= 2.25 m

Tides are semidiurnal= 706 tides/yr

T.E. = 0.5 x 706 tides/yr x .05 x 1.025 g/cm^3 x 980 cm/s x

2.25 $(cm)^2$ x 2.38E-11 Kcal/erg x 4186 J/Kcal x 10000 cm^2/m^2

5. Current energy, data from Deutsches Hyrdrographisches Institut (1960) adjusted for near shore region by factor of 0.145 x Ocean current (McClanahan, unpublished data).

Average current speed =14 cm/s

Average depth= 1.5 m

C.E.=0.5 x 1g/cm^3 x 14 cm/s^2 x 2.38E-11 erg/cal x 4186 J/Kcal x

depth (cm) x 14 cm/s x 3.1536 E7 s/yr x 100^2 cm^2/m^2

An absorption of 10% of the above energy was used as an estimate of the amount of kinetic energy absorbed by the reef bottom.

6. Rain, waves, sunlight and currents are all part of the same geobiospheric process. Therefore, in order to avoid double counting energy sources only the item with the largest value is included. Tides are part of another process and therefore tides and waves were summed in order to calculate the total emergy.
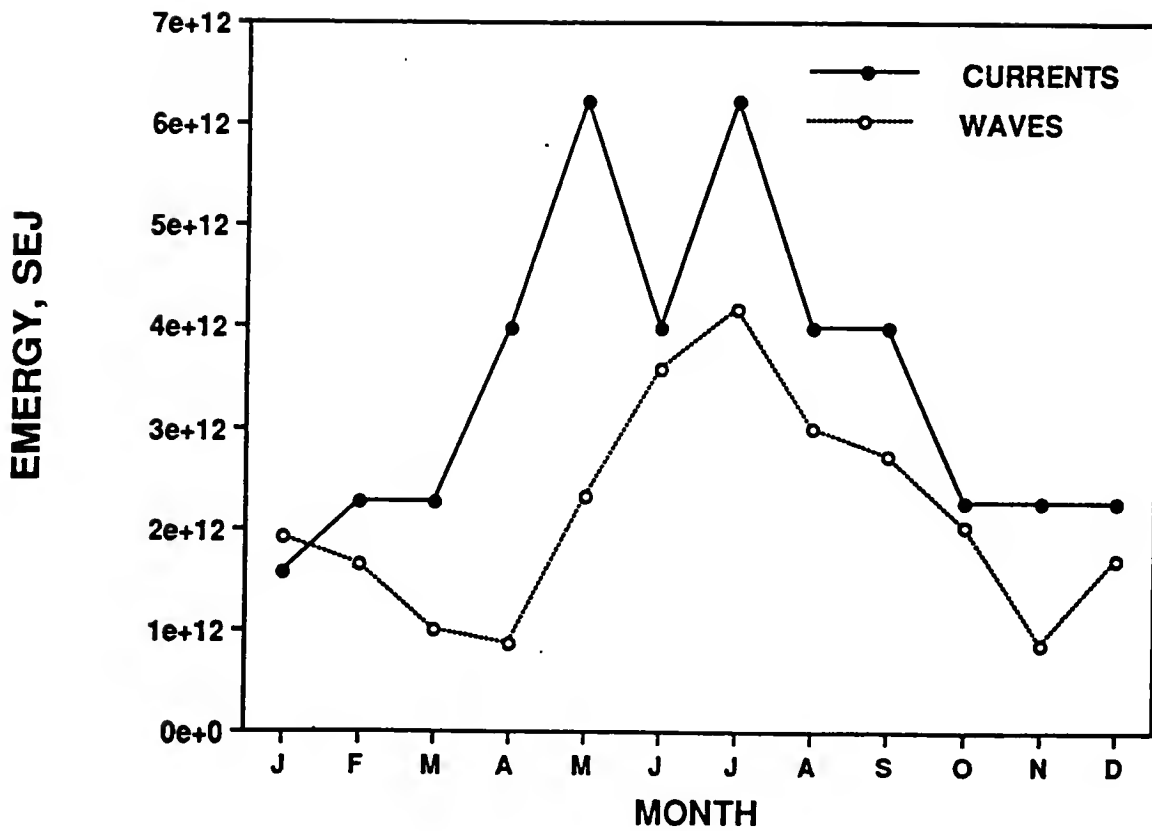
Fig. 6. Seasonal emergy inputs into the Kenyan coastline. Waves and currents are the two largest values, are very similar in magniture, and within the margin of error associated with transformities. The southeast monsoon occurs between April and September. SEJ=solar equivalent joules or the amount of solar energy required to produce this product.

Table 2. Solar transformities of major biological reef components. Based on 2.57E+13 sej/m^2/yr from Table 3.

Energy Type	Energy Joules/m^2/yr	Transformity sej/j	
1 Algal Production	2.14E+08	1.20E+05	2,57E13 sej
2 Coral Production	2.09E+07	1.23E+06	
3 Herbivorous Fish	1.36E+06	1.89E+07	
4 Sea Urchin Production	5.76E+06	4.46E+06	
5 Triggerfish Production	4.40E+04	5.84E+08	
6 Piscivorous Fish	1.57E+05	1.63E+08	
7 Fisheries Production	4.19E+04	6.13E+08	

1. Reef gross production varies between 2 and 12 gC/m^2/day with an average production of 8gC/m^2/day (Larkum 1983) and 70% algal cover
Production= 8 gC x 2.5 gC/gdw x 4 Kcal/gdw x 4186 J/Kcal x 2.5 gdw/g wet weight x 70% cover x 365 days/yr

2. Coral gross production about 5000 kcal/m^2/yr (Lewis 1981)

3. Maximum herbivorous fish biomass is 500 kg/ha (Goldman and Talbot 1976) and a gross P/B ratio of 6.5 (Chartock 1983).
Production=500 kg/ha x 1000 g/kg x .00001 ha/m^2 x 1 Kcal/g x 4186 J/Kcal x 6.5 kg/kg

4. Maximum sea urchin biomass is 500 g/m^2 (Muthiga and McClanahan 1987)
having a P/B ratio of 2.75 (Hawkins and Lewis 1982)
Production= 500 g/m^2 x 2.75 g/g x 1 Kcal/g x 4186 J/Kcal

5. Maximum triggerfish biomass is about 70 kg/ha with a P/B ratio of 1.5 (Polovina et al. 1984).

Production= 70 kg/ha x 1000 g/kg x 0.00001 m^2/ha x 1 Kcal/g
x 4186 J/Kcal x 1.5 kg/kg

6. Maximum piscivore production is about 250 kg/ha with P/B ratio
of 1.5 (Goldman and Talbot 1976).
Production= 250 kg/ha x 1000 g/kg x 0.00001 m^2/ha x 1 Kcal/g
x 4186 J/Kcal x 1.5 kg/kg

7. Fisheries production approximately 100 kg/ha (Smith 1978)
Production= 100 kg/ha x 1000 g/kg x 0.00001 m^2/ha x 1 Kcal/g
x 4186 J/Kcal

finally triggerfish. The transformity for reef fisheries production is 6.13E+8 (SEJ/J) solar equivalent joules/joule.

Seasonal Patterns of Energy Flow

The Kenyan coast is dominated by seasonal patterns of the Intertropical Convergence Zone (ITCZ) and its seasonal migration back and forth across the equator (McClanahan 1988). Two distinct seasons are created by this migration, the northeast monsoon (NEM) that occurs between October and March and the southeast monsoon (SEM) between March and October. Currents and sunlight are the largest energy sources followed by waves, tides, and the kinetic energy in rainfall, which is negligible (Fig. 6). During the southeast monsoon, currents, waves and rain are more important than during the northeast monsoon when sunlight is the major energy source. The northeast monsoon is typified by clear skies when the ITCZ has migrated away from the equator. Tidal energy is highest during the two intermonsoon periods. Total emergy (Fig. 7) is highest during the southeast monsoon and dominated by waves and current kinetic energy.
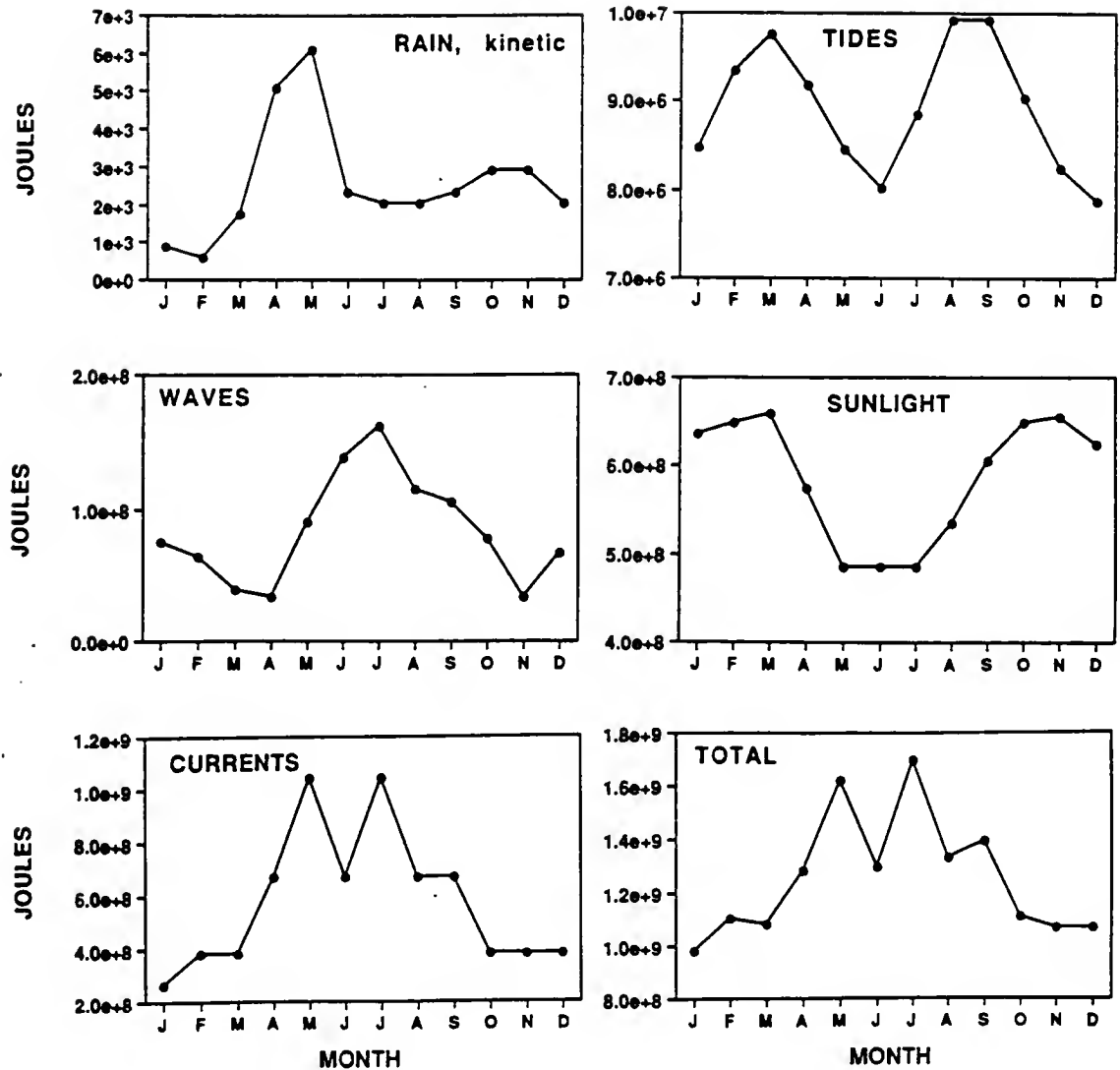
Fig. 7. Seasonal patterns of energy inputs into the coral reef environment of the Kenyan coastline. For source of data and calculations see Table 3. Current emergy flux is only partially absorbed (i.e. <10%) where as much larger fractions of the other energy sources are absorbed.

Community Structure

The Fish Assemblage

The absolute density of all studied fish families were significantly different between sites with the exception of the Diodontidae (Porcupine fish) and the Lagocephalidae (Puffers) which existed at low (<0.13 fish/100 m^2) densities at all sites (Table 3). The Pomacentridae (Damselfish) was the most abundant family but the abundance of other families depends upon the protected versus unprotected dichotomy. Reefs protected from fishing had significantly denser populations of all fish families with the exception of the Diodontidae and Lagocephalidae (Table 4). In terms of density, protected reefs had a predominance of the Pomacentridae, Acanthuridae (Surgeonfish), Labridae (Wrasses) and Scaridae (Parrotfish). The Pomacentridae and Labridae were most common in unprotected reefs; where the herbivorous Acanthuridae and Scaridae densities are greatly reduced. Data analyzed on a percentage basis resulted in similar patterns (Figs. 8 and 9) except in Bamburi and Diani where other families were also important. From observations, the Holocentridae were common in Bamburi and the Ostraciidae in Diani. Wilcoxon signed-rank tests comparing family densities between protected and unprotected reefs indicates rank differences in families for absolute density values ($z = -2.67$, $p < 0.01$) but not for relative densities ($z = -1.16$).

Table 3. Population densities (#/100 m^2, x ± S.D.) of the surveyed fish families, transect sample size and sampled area within the six studied sites. Kruskal-Wallis tests of significance between sites are included. NS=not significant, ** p<0.01.

Fish Family	Malindi	Watamu	Vipingo	Kanamai	Bamburi	Diani	Kruskal Wallis Test
Transects, n=	5	3	5	3	5	5	
Area sampled, m2	2500	1500	2500	1500	2500	2500	
Acanthuridae	15.4 ± 5.2	12.8 ± 2.9	1.2 ± 1.0	0.07 ± 0.09	1.3 ± 0.7	0.4 ± 0.5	**
Balistidae	0.9 ± 0.3	0.3 ± 0.1	0.08 ± 0.1	0.0 ± 0.0	0.12 ± 0.16	0.04 ± 0.08	**
Chaetodontidae	2.8 ± 1.7	0.7 ± 0.3	0.8 ± 0.7	0.4 ± 0.3	0.16 ± 0.23	0.64 ± 0.46	**
Diodontidae	0.0 ± 0.0	0.06 ± 0.09	0.08 ± 0.10	0.07 ± 0.09	0.04 ± 0.08	0.0 ± 0.0	NS
Labridae	11.4 ± 5.1	11.3 ± 2.7	6.0 ± 4.2	6.5 ± 2.5	2.7 ± 1.1	4.2 ± 1.7	**
Lagocephalidae	0.0 ± 0.0	0.13 ± 0.19	0.0 ± 0.0	0.0 ± 0.0	0.06 ± 0.16	0.0 ± 0.0	NS
Lutjanidae	1.4 ± 0.8	6.2 ± 7.4	0.0 ± 0.0	0.0 ± 0.0	0.04 ± 0.08	0.0 ± 0.0	**
Pomacanthidae	0.2 ± 0.2	0.7 ± 0.3	0.04 ± 0.08	0.0 ± 0.0	0.08 ± 0.16	0.04 ± 0.08	**
Pomacentridae	66.0 ± 20.2	73.3 ± 25.6	25.7 ± 8.2	25.1 ± 7.0	18.7 ± 6.0	9.1 ± 2.0	**
Scaridae	10.0 ± 4.9	8.3 ± 4.6	6.0 ± 4.1	1.1 ± 0.8	0.5 ± 0.5	0.5 ± 0.4	**
Others	9.2 ± 4.4	15.1 ± 8.4	3.4 ± 1.4	2.5 ± 1.7	5.3 ± 3.1	3.4 ± 1.3	**

Table 4. Density (#/100m^2, x $\pm$ S.D.) comparisons of the major fish families found within the two protected marine parks (Malindi and Watamu, n=8) and the four unprotected reefs (Vipingo, Kanamai, Bamuburi and Diani, n=18). Mann-Whitney U-test of significance includes U value and level of significance. NS = not significant

Fish Family	Protected	Unprotected	Mann-Whitney U-test	
Acanthuridae	14.4 $\pm$ 4.6	0.81$\pm$ 0.85	144	p<0.001
Balistidae	0.70 $\pm$ 0.37	0.07 $\pm$ 0.12	140	p<0.001
Chaetodontidae	2.03 $\pm$ 1.69	0.51 $\pm$ 0.54	123	p<0.005
Diodontidae	0.025 $\pm$ 0.066	0.044 $\pm$ 0.083	83.5	NS
Labridae	11.4 $\pm$ 4.4	8.9 $\pm$ 8.5	105	p<0.05*
Lagocephalidae	0.05 $\pm$ 0.13	0.06 $\pm$ 0.16	73	NS
Lutjanidae	3.2 $\pm$ 5.1	0.01 $\pm$ 0.04	144	p<0.001
Pomacanthidae	0.38 $\pm$ 0.35	0.04 $\pm$ 0.08	117	p<0.01
Pomacentridae	68.7 $\pm$22.6	19.1 $\pm$ 9.2	144	p<0.001
Scaridae	9.3 + 4.9	2.1 $\pm$ 3.3	132	p<0.001
Others	11.4 $\pm$ 6.8	3.8 $\pm$ 2.3	127	p<0.001
Total	121.6 $\pm$ 31.4	35.4 $\pm$ 19.4	144	p<0.001

* Significant only for a one-tailed test
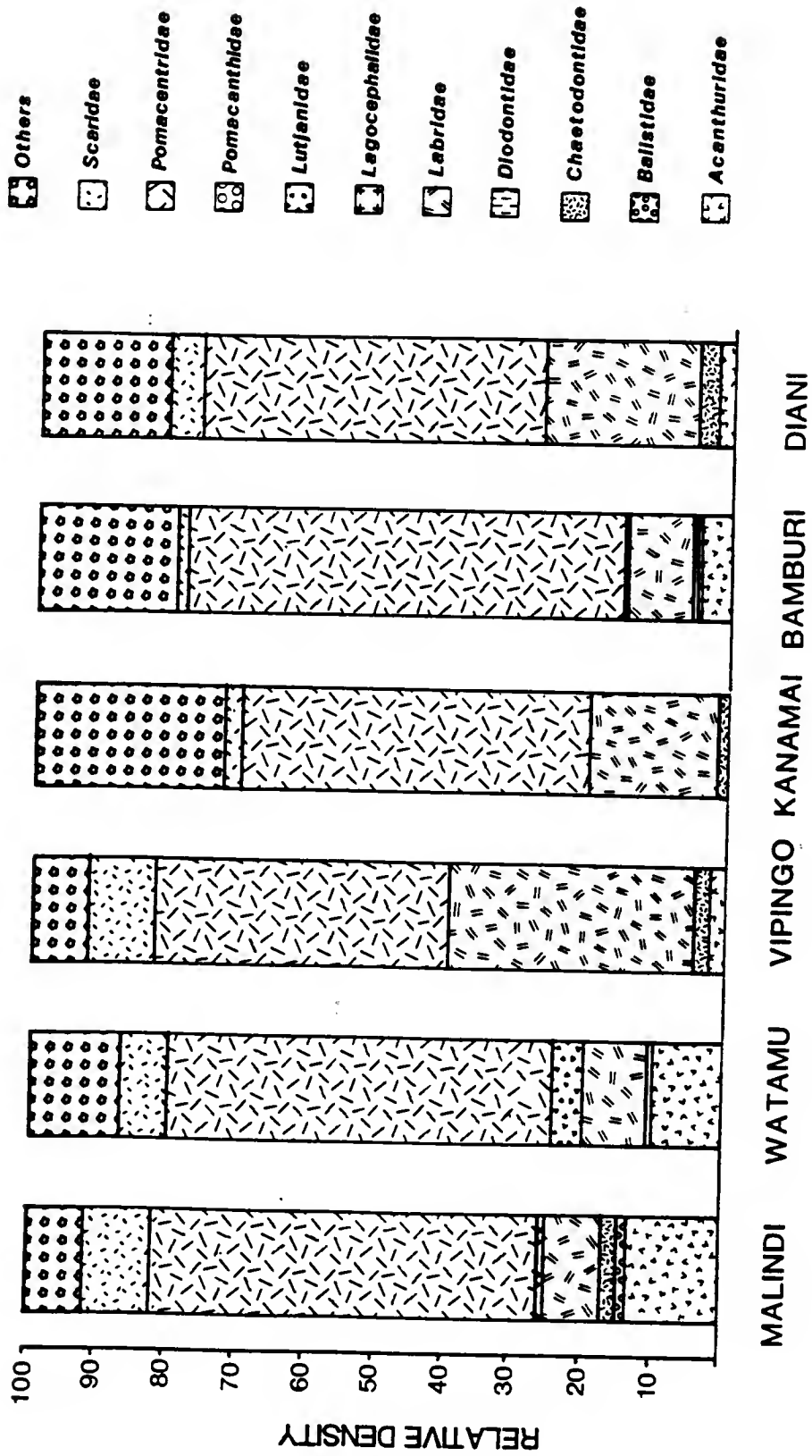
Fig. 8. Relative importance (on a density basis) of fish families studied at the six sites.
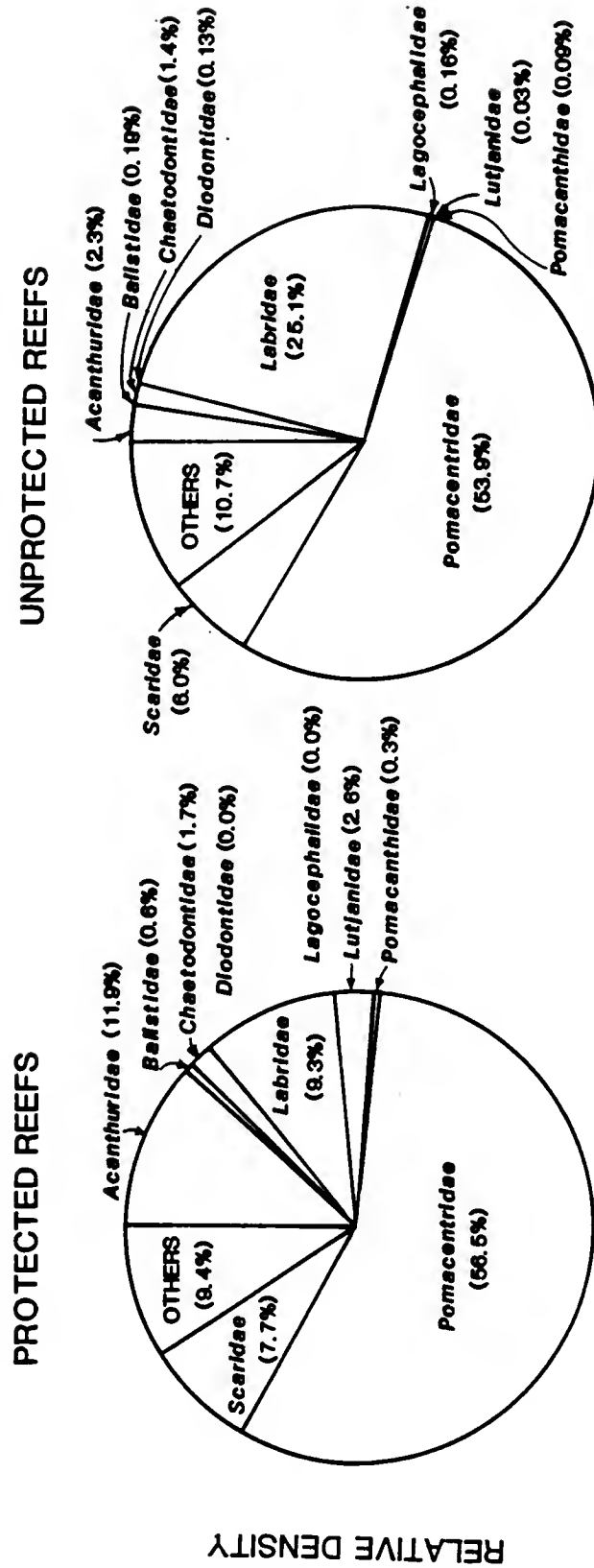
Fig. 9. Relative density of fish families in protected and unprotected reef lagoons.

With the exception of the Lagocephalidae there were fewer fish on the unprotected reef, particularly in the larger size classes (Fig. 10). The Labridae which were only slightly more densely populated in protected reefs, had smaller individuals in unprotected reefs (G-test, G=9.94, p<0.05). Other (i.e. unclassified) families were most important in protected reefs (Tables 3 and 4) and included the Siganidae (Rabbitfish), Serranidae (Groupers), Lethrinidae (Snappers), Aulostomidae (Trumpetfish), Holocentridae (Squirrelfishes) and Apogonidae (Cardinalfishes). Other families in unprotected reefs included the Holocentridae, Ostraciidae (Trunkfishes) and Apogonidae. Although a species level analysis was not quantified, there appeared to be greater species diversity in protected reefs.

Both Principal Component Analysis (PCA) and cluster analysis of fish families (Fig. 11) indicate distinct differences between protected and unprotected reef communities. The first axis of the PCA separated the protected from the unprotected reefs whereas the second axis separated the two protected reefs. This indicates that protected and unprotected reef family composition differ based on this managment distinction. Eighty-nine percent of the variation was accounted for by these two axes. Cluster analysis also indicates 90% similarity between protected reefs but 60% similarity between protected and unprotected reefs. Among unprotected reefs Kanamai and Vipingo were similar (90%). Diani was the least similar site among the unprotected reefs.

Fish populations in all trophic levels were less abundant in unprotected reefs (Fig 12a). The analysis based on relative density
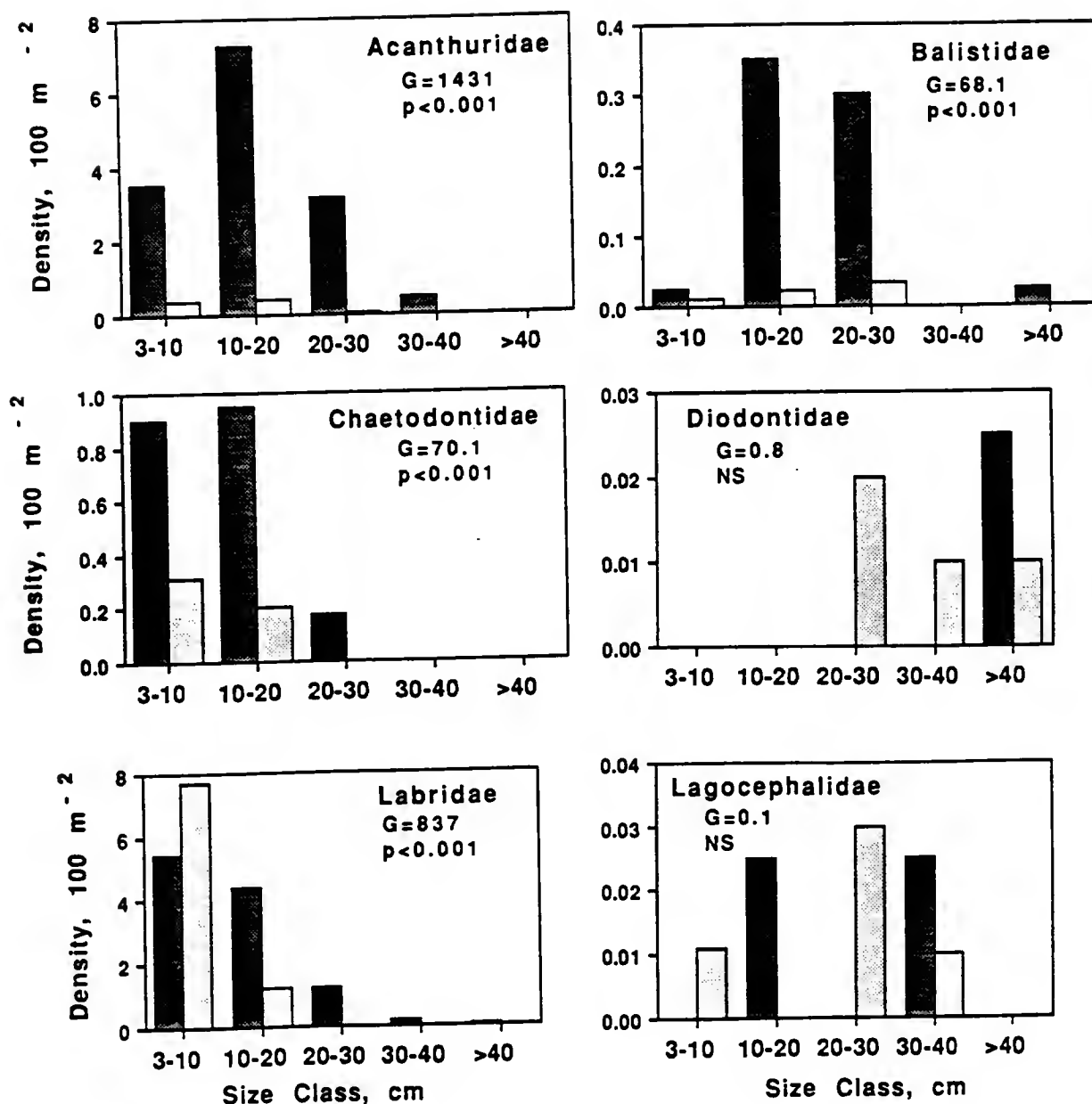
Fig. 10. Size class frequency distribution of the measured fish families in protected versus unprotected reefs. Size class I = 3 to 10 cm, II = 10 to 20 cm, III = 20 to 30 cm, IV = 30 to 40 cm, V = >40 cm. Dark-shaded bars refer to the protected reefs and light-shaded bars to unprotected reefs.
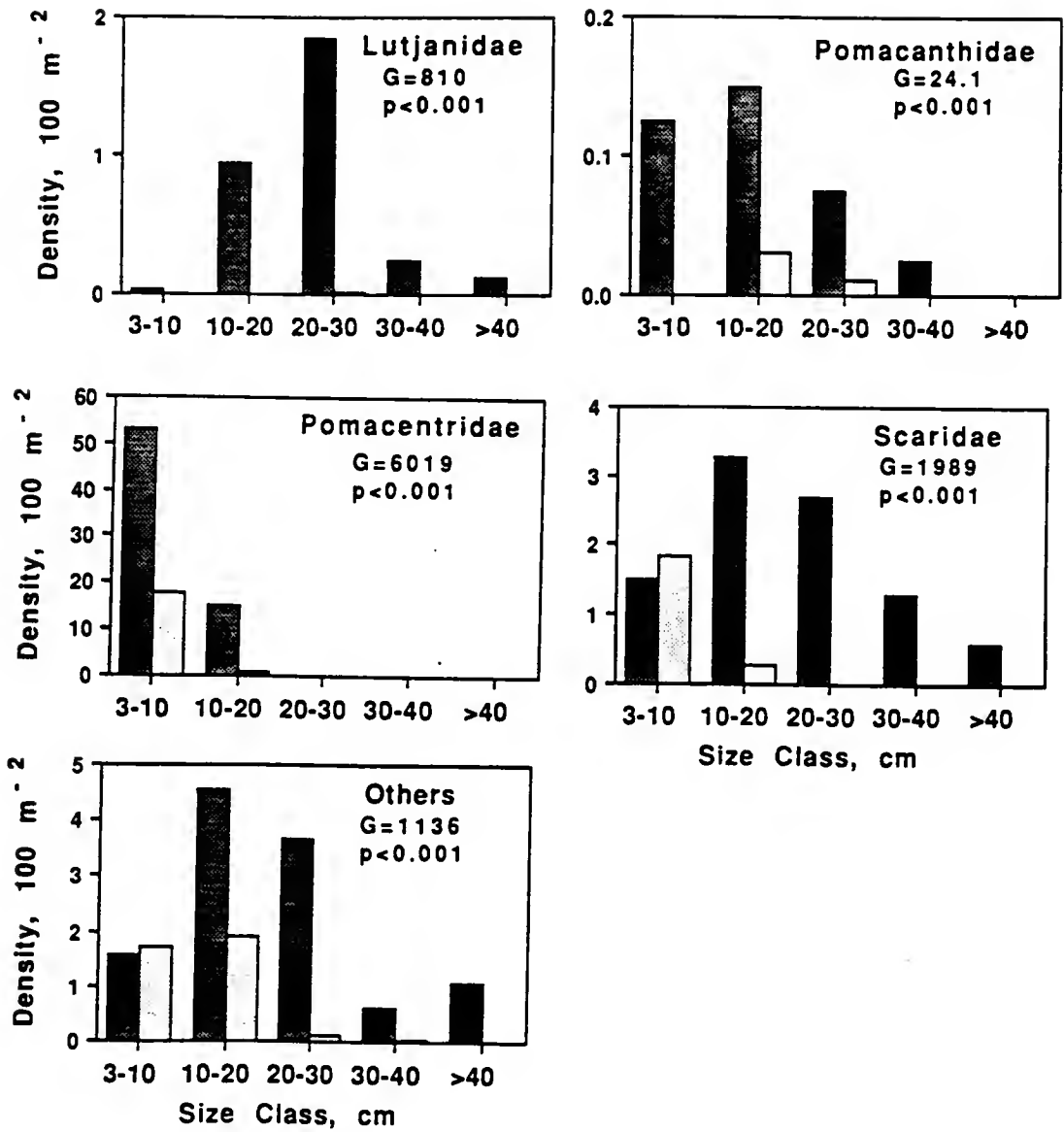
Figure 10. continued
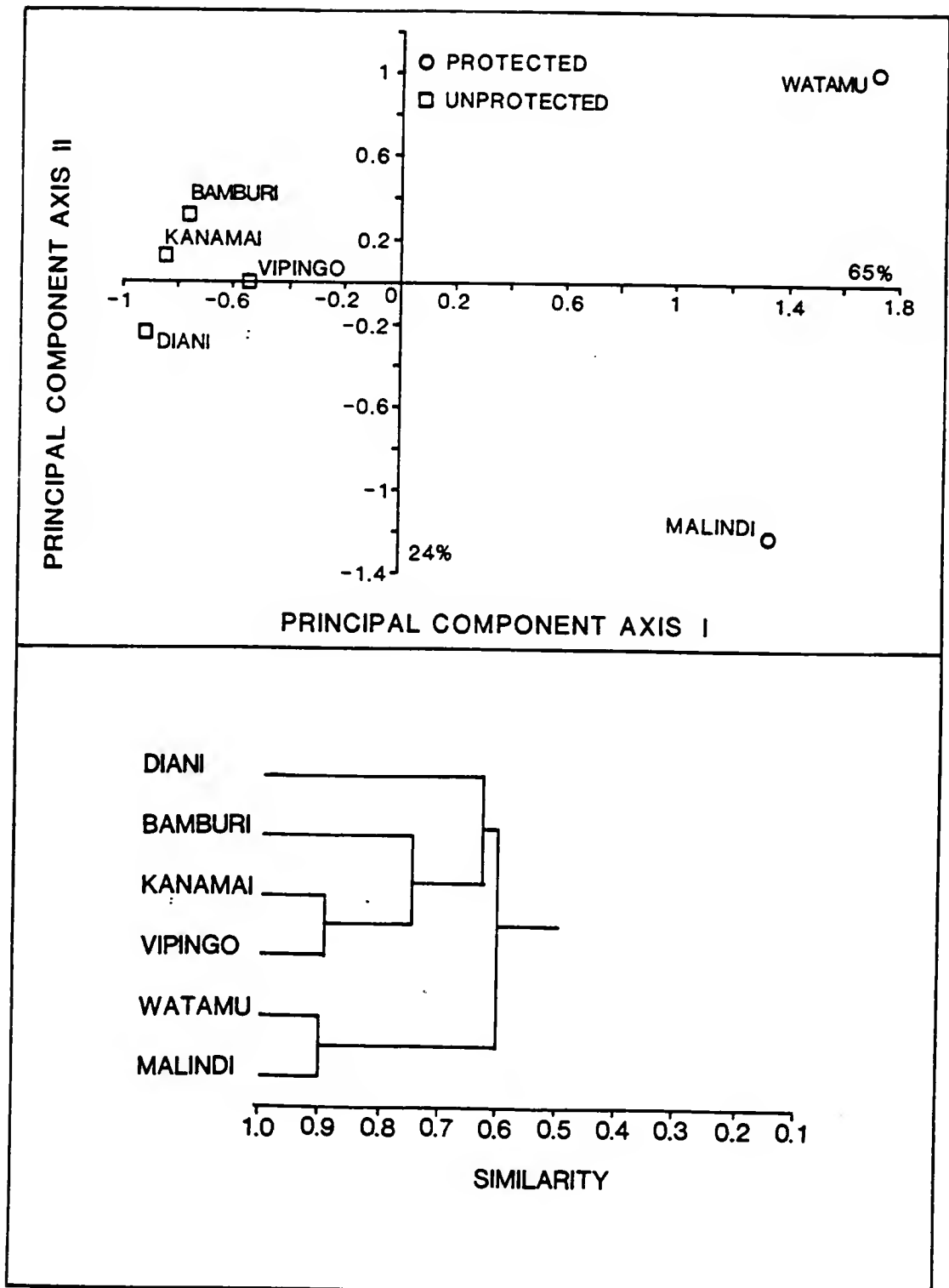
Fig. 11. Cluster analysis and Principal Component Analysis (showing the first two principal components) of the six studied sites (o = protected and = unprotected sites) based on family densities. Cluster analysis uses the Bray-Curtis (1957) measure of similarity and average between-group linkages.

Fig. 12. Absolute (a) and relative abundance (b) of major trophic groups comparing protected and unprotected reefs. Herbivores include the Acanthuridae and Scaridae, Omnivores include the Pomacentridae, Pomacanthidae and Chaetodontidae, Carnivores are principally invertebrate-feeders and include the Balistidae, Diodontidae, Labridae, Lagocephalidae and Lutjanidae.
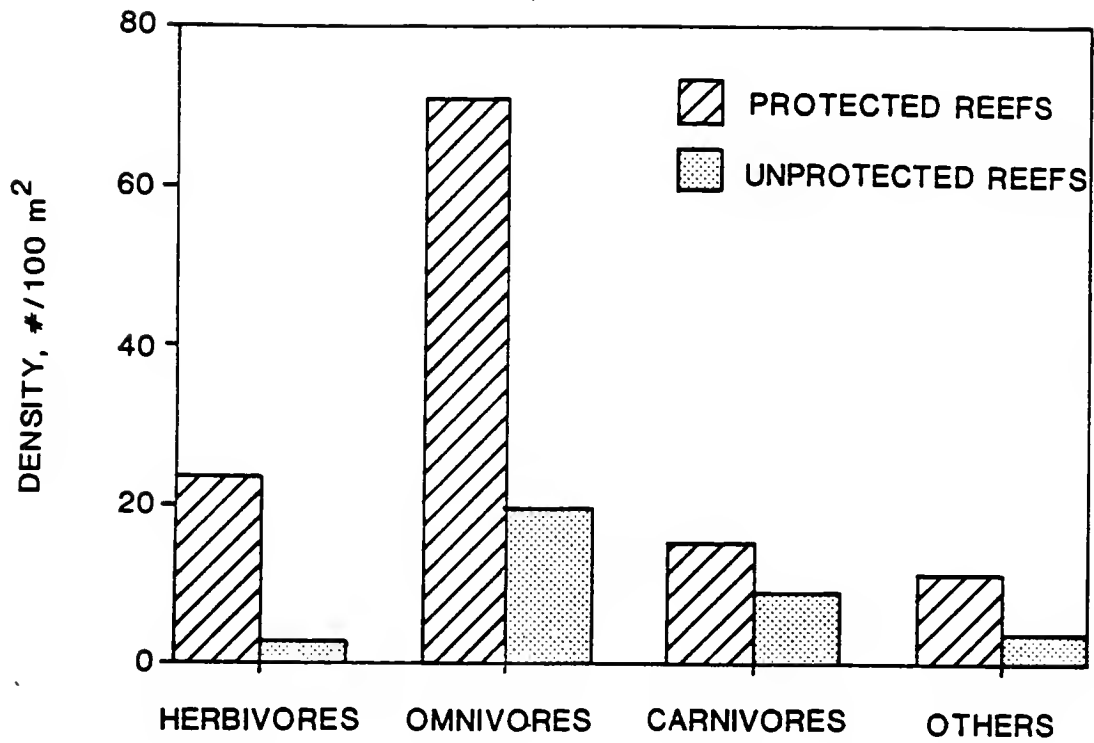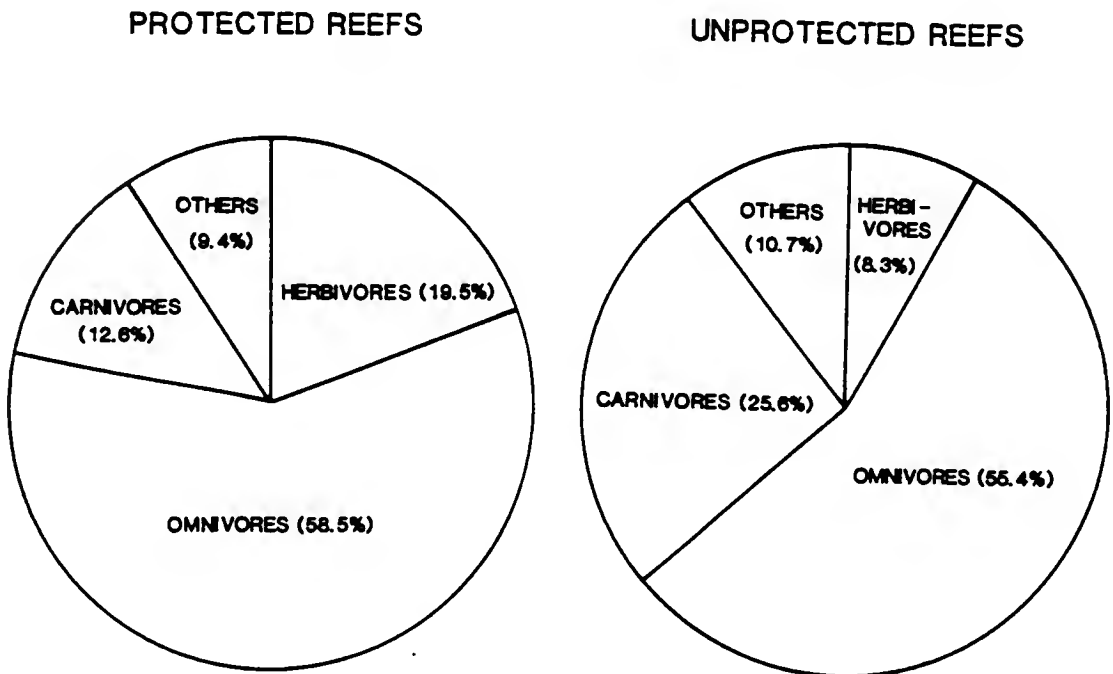
indicates fewer herbivores fish and more invertebrate carnivores (Fig. 12b). Most of the carnivore group feed on invertebrates. The unclassified group was about 10% by density and mostly composed of carnivores with the exception of a few Siganidae, Blenniidae (Blennies) and Gobiidae (Gobies).

The Sea Urchin Assemblage

Density and diversity measurements of sea urchins indicate large differences between the six studied reefs (Table 5) and between protected and unprotected reefs (Table 6). Protected reefs had low sea urchin population densities and diversity (Fig. 13). Species-area curves for the protected reefs included only the three species *Echinostrephus molaris*, *Echinometra mathaei* and *Echinothrix calamaris*. *E. mathaei* in protected reefs were very small (i.e. <1.5 cm test width). In contrast, 10 species of sea urchin were found in unprotected reefs and principally included *Diadema savignyi, D . setosum, Tripneustes gratilla* and *Echinothrix diadema* not found in protected reefs. Cluster analysis (Fig. 14) of the sea urchin assemblage showed protected and unprotected reefs as two distinct groups.

Biomass of dominant sea urchins on each reef was calculated from average lengths and length-weight correlations (Table 7); weights of the rarer species were estimated. Much more urchin biomass (3 orders of magnitude) was found on all the unprotected

Table 5. Sea urchin densities (x ± S.D.) per 10 m^2, the number of sites, sample sizes and area sampled in the six locations. Kruskal-Wallis test of difference between reefs and level of significance provided. Survival given days for a possible maximum of 3 days. NS = not significant.

	Malindi	Watamu	Vipingo	Kanamai	Bamburi	Diani	Kruskal-Wallis
Sites n=	2	1	3	3	3	2	
Quadrats, n=	15	9	27	27	24	18	
Area sampled, m^2	375	225	270	675	420	450	
Diadema savignyi	0.0	0.0	12.9 ±7.6	3.4 ±4.0	6.3 ±6.3	0.2 ±0.5	p < 0.001
Diadema setosum	0.0	0.0	3.7 ±3.7	2.3 ±1.9	0.5 ±0.8	0.02 ±0.9	p < 0.001
Echinometra mathaei	0.2 ±0.3	0.2 ±0.4	32.6 ±20.7	80.6 ±53.9	10.8 ±7.1	135.0 ±123.0	p < 0.001
Echinostrephus molaris	0.3 ±0.4	0.1 ±0.3	1.1 ±1.3	0.2 ±0.3	10.7 ±8.1	0.5 ±0.7	p < 0.001
Echinothrix calamaris	0.03 ±0.10	0.0	0.6 ±0.9	0.7 ±0.7	11.1 ±9.1	0.3 ±0.6	p < 0.001
Echinothrix diadema	0.0	0.0	0.1 ±0.3	0.0	0.4 ±0.5	0.02 ±0.1	p < 0.001
Prinocidaris sp.	0.0	0.0	0.0	0.03 ±0.11	0.0	0.0	NS
Stomopneustes variolaris	0.0	0.0	0.04 ±0.19	0.0	0.1 ±0.3	0.0	NS
Toxopneustes pileolus	0.0	0.04 ±0.13	0.2 ±0.4	0.0	0.2 ±0.4	0.02 ±0.1	p < 0.005
Tripneustes gratilla	0.0	0.0	8.2 ±5.7	8.9 ±8.2	1.3 ±1.4	5.9 ±8.2	p < 0.001
Total	0.8 ±1.2	0.4 ±0.6	59.4 ±25.8	60.0 ±57.4	41.4 ±23.5	141.4 ±120.4	p < 0.001
Survival	0.36 ±0.10	0.48 ±0.15	1.07 ±0.13	2.31 ±0.12	1.25 ±0.13	2.32 ±0.15	p < 0.001

Table 6. Total sea urchin densities and survival rates (in days) of *Echinometra mathaei* (see methods) for protected and unprotected locations. The significance level of a Mann-Whitney U test of difference between protected and unprotected locations is provided.

	Protected	Unprotected	Mann-Whitney U test
Total sea urchin density, #/10m²	0.45±0.12	80.70 ±7.30	p < 0.001
Survival, days	0.40 ±0.08	1.68±0.07	p < 0.001
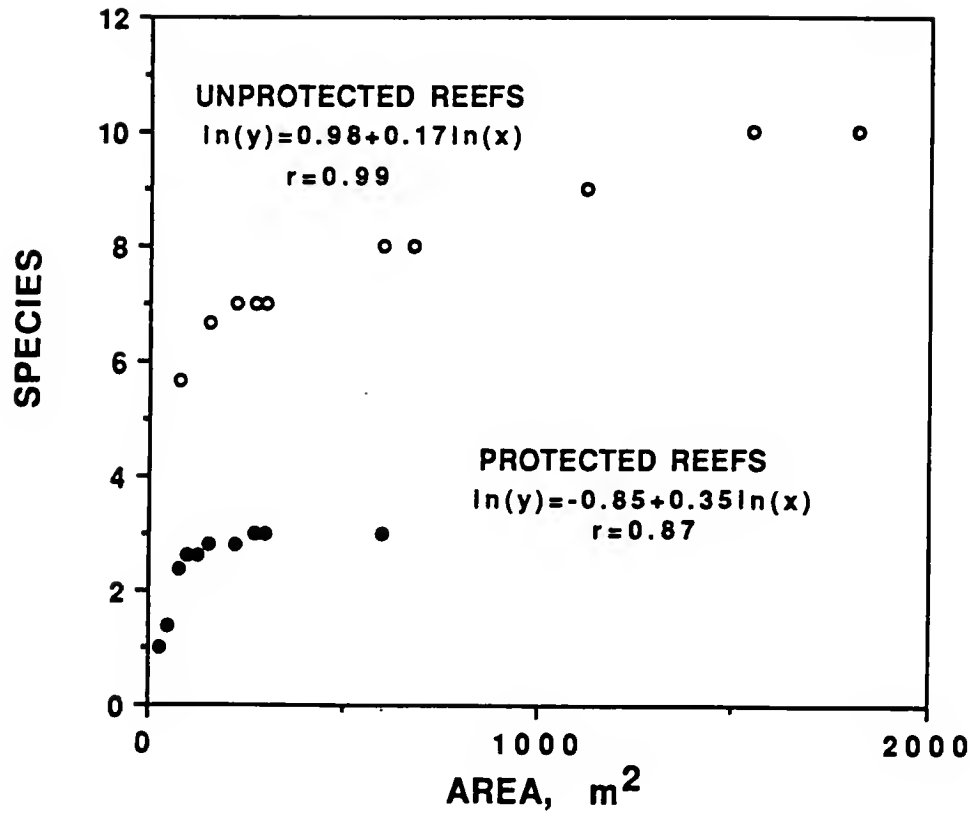
Fig. 13. Species-area curves for Kenyan reef lagoon sea urchins comparing protected and unprotected reefs.
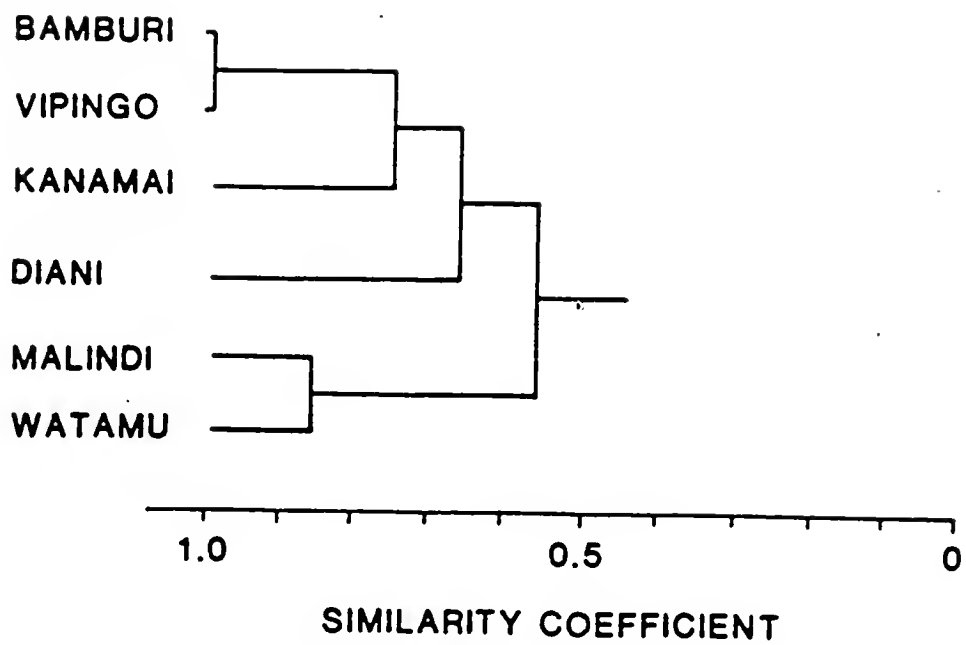
Fig. 14. Cluster analysis of the sea urchin assemblage using the Bray-Curtis (1957) measure of similarity and average between-group linkages.

Table 7. Length-weight correlations (mm versus grams) of 4 major sea urchin species, an approximate average length and weight and estimated average weight of 2 less abundant species. r= correlation coefficient and n is number of individuals in the sample.

Species	Length-Weight	r	n	Average Length mm	Average Weight grams
Echinometra mathaei	$y=0.002x^{2.64}$	0.96	144	40	33.9
Tripneustes gratilla	$y=0.00062x^{2.90}$	0.91	73	64	109
Diadema savignyi	$y=0.005x^{2.47}$	0.97	50	60	125
Diadema setosum	$y=0.003x^{2.57}$	0.90	61	67	150
Echinostrephus molaris				25	10
Echinothrix calamaris				150	500

reefs than protected reefs (Fig. 15). Among unprotected reefs biomass was similar.

An analysis of the sea urchin's species composition in unprotected reefs by the rank-abundance technique (Fig. 16) indicates a geometric or logseries (Odum *et al.* 1960, May 1975) distribution. There was a positive relationship between the sea urchin's adult body size and it species rank (Fig. 17a) and a left-skewed distributional relationship between body size and abundance (Fig. 17b).

Sea urchin coexistence

An analysis of coexistence between the three most abundant species within Kanamai reef indicates similar across-reef distribution patterns (Fig. 18) with *E. mathaei* being the most abundant species followed by *D. savignyi* and lastly *D. setosum*. Despite these similarities, it is clear that each species has microspatial preferences within the reef (Table 8). *E. mathaei* inhabited small crevices, *D. savignyi* inhabits intermediate crevices and occasionally small social groups, and *D. setosum* was occasionally found in large crevices but most frequently in the open in social groups. Crevice habitation and sociality appear to be closely related to body size and morphology (Table 8 and Fig. 19), the smaller the species the more frequently they were found in crevices. The smaller their spine length, the less their sociality. A day-night comparison (Table 9) indicates that *D. setosum* leaves crevices and reduces its social group size at night presumably because of nocturnal grazing. The other two species

SEA URCHIN BIOMASS IN SIX KENYAN REEF LAGOONS
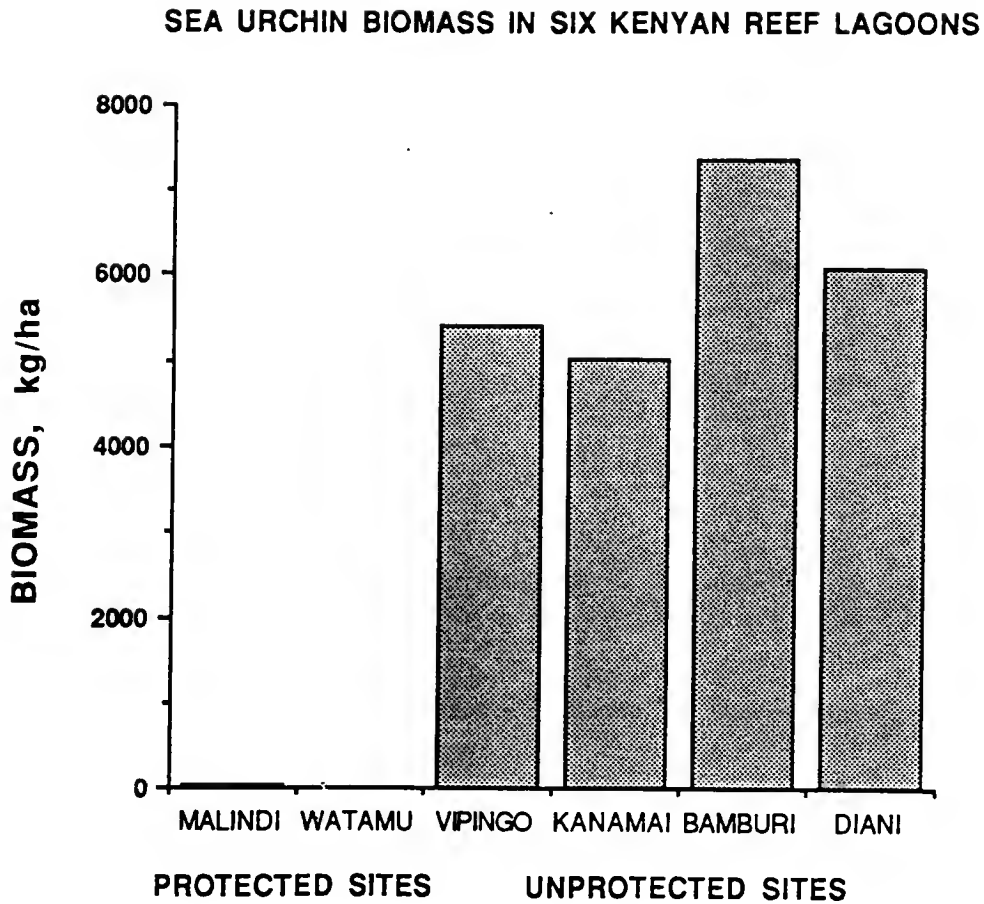
Fig. 15. Estimated sea urchin biomass in the six studied Kenyan reef lagoons. Estimates based on average weights (Table 7) and densities of each species.
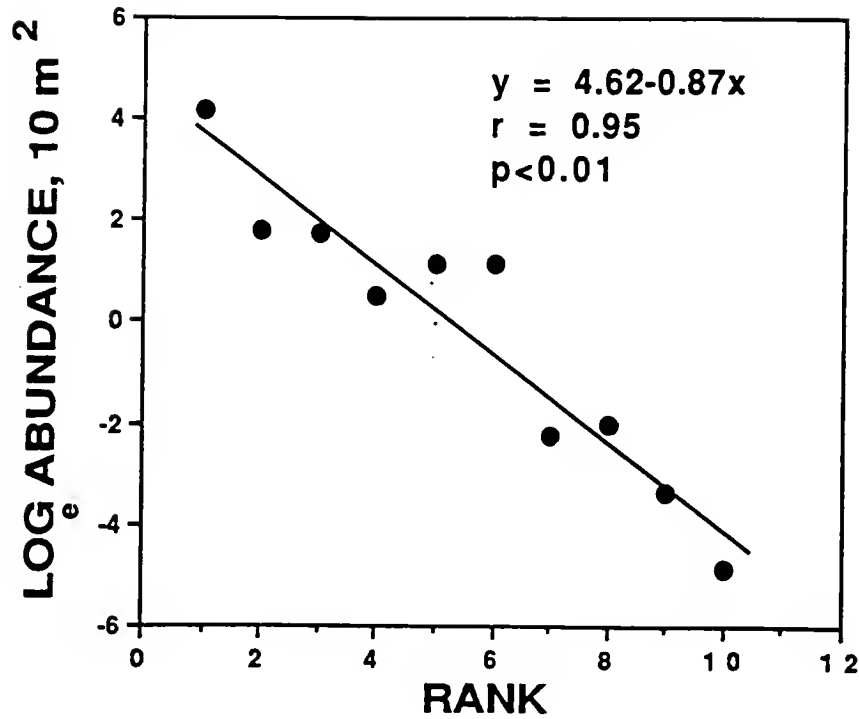
Fig. 16. Species rank plotted against the log abundance of the sea urchins found within unprotected Kenyan reef lagoons. Data taken from unprotected reefs in Table 5.
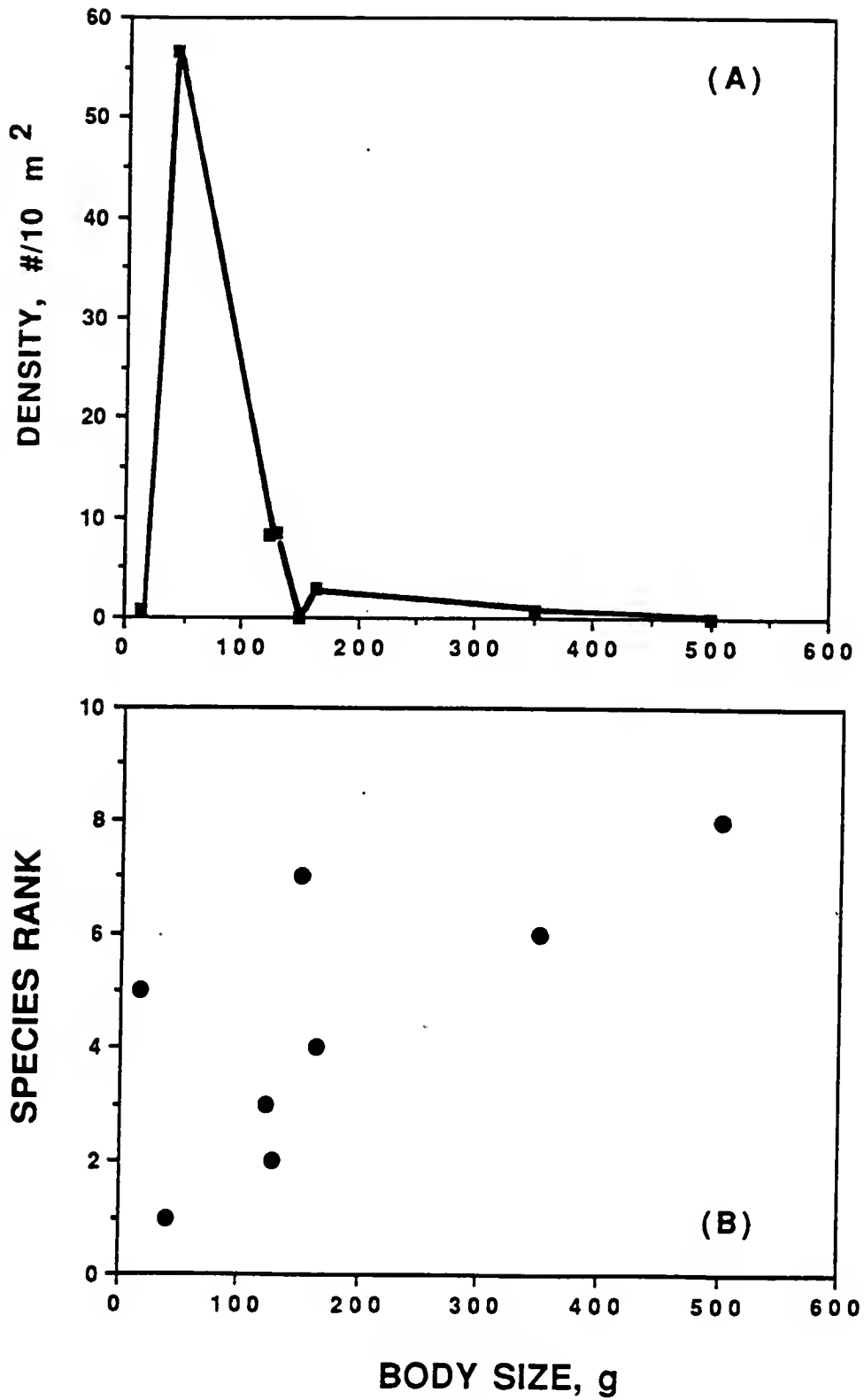
Fig. 17. The relationship between sea urchin body size and (a) density and (b) species rank from unprotected Kenyan reef lagoons.
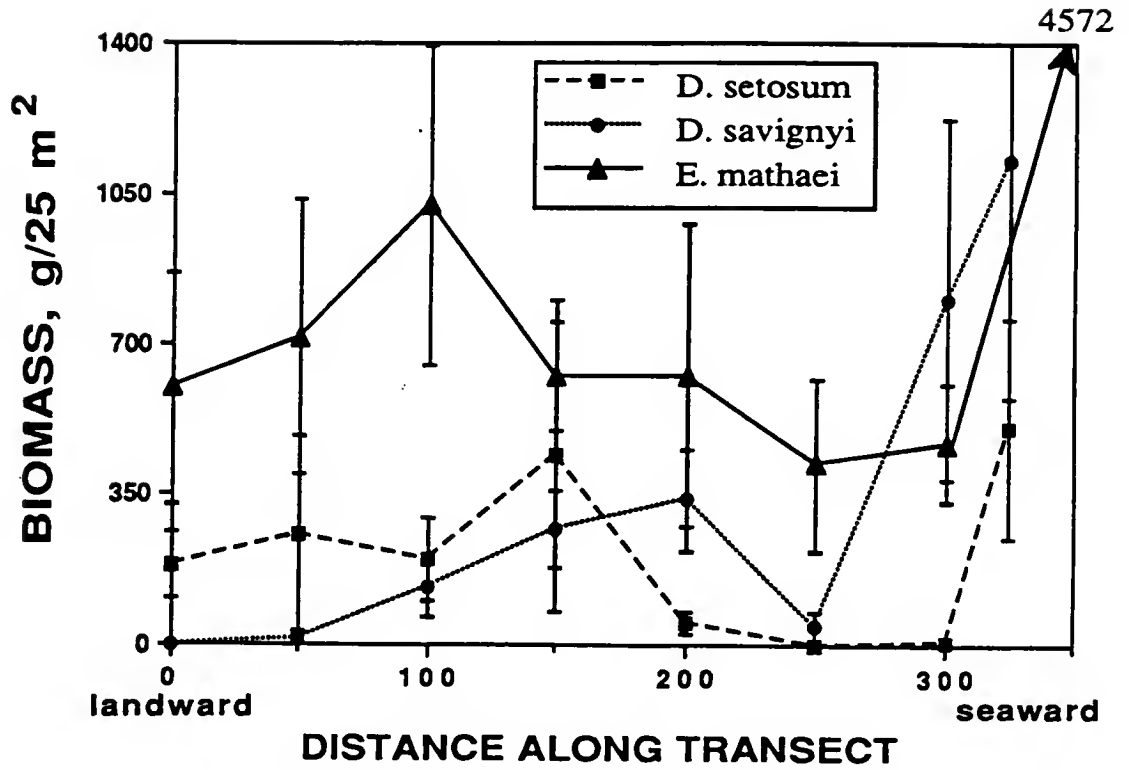
Fig. 18. Biomass distribution of the three sea urchin species across the Kanamai reef lagoon. Bars represent ± 1 standard error of the mean (s.e.m.)

Table 8. Morphometric and behavioral data (x ± S.D.) collected on the three sea urchin species in eighty quadrats inhabiting the Kanamai reef lagoon.

Measurement	E. mathaei	D. savignyi	D. setosum
Test length, mm	41.3 ± 3.4	59.8 ± 7.6	67.4 ± 7.8
Spine Length, cm	2.1 ± 0.2	9.3 ± 1.8	12.7 ± 2.3
Inhabiting Crevices, %	80.6 ± 35.2	83.9 ± 22.0	23.7 ± 37.6
Crevice width, cm	4.6 ± 1.7	12.9 ± 4.5	19.4 ± 6.9
Within groups, %	0.0 ± 0.0	18.3 ± 31.6	32.7 ± 40.6
Group size, #	1.0 ± 0.0	1.2 ± 0.3	2.2 ± 2.2
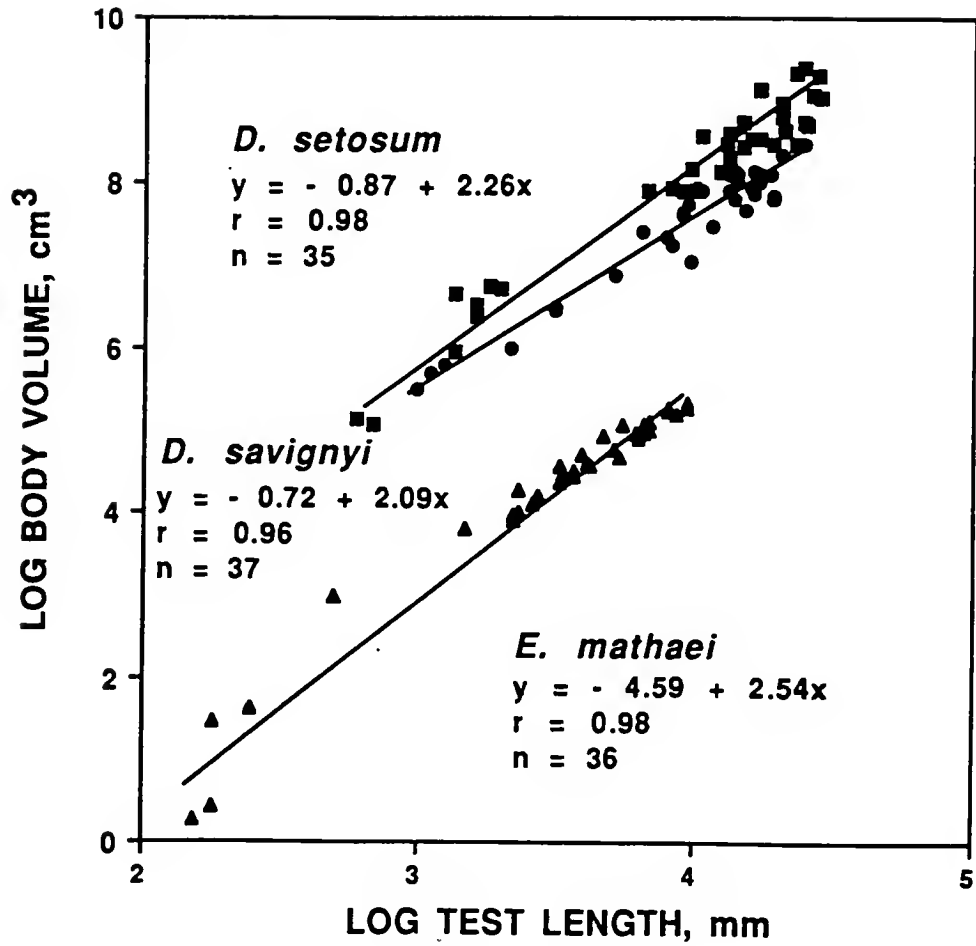
Fig. 19.Test length-body volume (test + spines) relationships for the three sea urchin species.

Table 9. A day-night comparison of crevice habitation and social behavior of the three sea urchin species (n=56 individuals/species). Social groups included individuals from other species. Statistical significance for crevice fidelity determined by a G-test and group size by a Mann-Whitney U-test. * = p<0.05, **=p<0.01.

Species	Within crevices, %		Group size	
	Day	Night	Day	Night
E. mathaei	60.7	66.1 NS	0.0	0.0 NS
D. savignyi	76.8	73.2NS	2.6±0.5	1.8±0.2*
D. setosum	62.5	28.6 **	3.5±0.4	2.8±0.3*

showed less diurnal changes. Apparently, nocturnal foraging by *D. setosum* reduced the frequency of *D. setosum* in the *D. savignyi* groups and therefore the average nocturnal group size.

Competition and predation

Competition experiments for shelter and space indicate that *E. mathaei* exhibited intra- and interspecific agonistic behavior (Table 10). In competition for shelter "wins" consistently went to initial *E. mathaei* inhabitants. Interspecific competition experiments indicated that *E. mathaei* consistently won interspecific competition with *Diadema* regardless of the initial or addition sequence.

Competitive interactions among and between *Diadema* species were clarified by the experiment with reduced shelter sizes. When shelter sizes were halved, larger individuals acquired better shelter positions (Table 11). In interspecific competition experiments using randomly selected individuals, *D. setosum* was the top competitor but probably because *D. setosum* is larger on average than *D. savignyi*. Where *D. savignyi* had similar or larger body lengths or volumes than *D. setosum, D. savignyi* was the superior competitor in interspecific interactions.

Comparisons of predator susceptibility suggest that *E. mathaei* is most susceptible to predation when it is outside its burrows, but burrow habitation greatly improves its survival probability (Table 12). Most *Diadema* survived the experiment's duration. Differences in survival of *Diadema* species were not statistically significant. Sociality may have improved *D. setosum* survival in Kanamai

Table 10. Results of the intra- and interspecific competition of urchins for large (16 cm wide) crevices. Control results give the total number of solitary individuals that remained within (Ni) or evacuated (No) crevices during a 15-minute interval. Experimental results give the frequency of individuals remaining in (fi) or leaving (fo) crevices after a 15-minute period of interaction between initial and addition animals. The effect of the interaction (positive or negative), the adjusted G value and the level of significance are given for comparisons between controls and experiments for each initial and addition animal. See text for experimental details.

Species tested	Controls					Species Added	Experiments					G-test	
							Initial			Addition			
	N	Ni	No	fi	fo		N	fi	fo	fi	fo	Initial	Addition
E. mathaei	49	48	1	0.98	0.02	*E. mathaei*	15	14	1	1	14	-1.0 NS	-98.9 ***
						D. savignyi	15	15	0	6	9	+2.8 NS	-9.1 **
						D. setosum	20	19	1	7	13	-0.6 NS	-11.5 ***
D. savignyi	43	33	10	0.77	0.23	*D. savignyi*	15	14	1	14	1	+1.0	+1.0 NS
						E. mathaei	16	5	11	16	0	-14.6 ***	+2.8 NS
						D. setosum	15	9	6	9	6	-2.1 NS	-1.0 NS
D. setosum	47	34	13	0.72	0.28	*D. setosum*	15	11	4	11	4	+0.0 NS	+0.0 NS
						E. mathaei	32	16	16	32	0	-6.8 **	+2.1NS
						D. savignyi	15	15	0	13	2	+7.3	+0.9 NS

Table 11. Results of competition for small (8 cm wide) crevices between *Diadema setosum* and *D. savignyi* and intraspecific competition within *D. savignyi*. Experiments compare the number of "wins", where wins are designated to the individual with the greatest percentage of test hidden beneath the crevice, and the percentage of test (x ± s.e.m.) hidden beneath crevices. Experiment 1 compares randomly selected *D. setosum* and *D. savignyi*. Experiment 2 compares intraspecific competition between different size *D. savignyi* individuals. Experiment 3 compares competition between *D. savignyi* and *D. setosum* where *D. setosum* body (test) size and body volume (test +spines) are smaller than *D. savignyi*. Ne = number of experiments, Ni=number of wins per category. A G-test was used for differences between wins and a Mann-Whitney U-test for the percentage of hidden test. *=p<0.05, **=p<0.01.

Experiment, competitors	Ne	Wins Ni	Gadj	Hidden Test, % x ± s.e.m.
1. *D. setosum* with	24	18		61.3 ± 7.8
D. savignyi		6	6.15 *	26.7 + 7.8 **
2. *D. savignyi* intraspecific				
Larger individuals with	24	17		57.9 ± 8.5
Smaller individuals		7	4.2 *	38.3 ± 8.6 *
3. Body size				
Small *D. setosum* with	30	9		33.4 ± 7.2
larger *D. savignyi*		21	4.85 *	61.0 ± 7.2 **
Body volume				
Small *D. setosum* with	16	2		20.6 ± 7.8
larger *D. savingyi*		14	9.81	71.9 ± 9.3 **

Table 12. Survival rates in days (x ± S.D.) for the three sea urchin species for a five day period. Experiments were undertaken at two sites (Kanamai and Vipingo) and include a statistical comparison of survival between solitary and social groups for the two *Diadema* species and between burrowed and unburrowed individuals for *Echinometra mathaei*. The number of individuals for each category is given in parentheses. + = p<0.10, *=p<0.05, ** = p<0.01.

	Kanamai	Vipingo	Site Totals
D. setosum			
Social	4.6 ± 1.0 (42)	4.8 ± 0.8 (24)	4.7 ± 1.0 (66)
Solitary	3.6 ± 2.1 (29)	4.7 ± 1.1 (15)NS	3.9 ± 1.9 (44)+
Species total			4.4 ± 1.4 (110)
D. savignyi			
Social	4.7 ± 1.1 (26)	4.8 ± 1.0 (24)	4.7 ± 1.0 (50)
Solitary	4.6 ± 1.3 (29)	5.0 ± 0.0 (15)NS	4.7 ± 1.1 (44)NS
Species total			4.7 ± 1.1 (99)
E. mathaei Exposed			
Exp. 1	3.3 ± 2.1 (34)	1.9 ± 1.6 (29)	2.9 ± 2.1 (88)
Exp. 2	3.3 ± 2.1 (25)		
E. mathaei Burrowed			
Exp. 1	4.3 ± 2.1 (18) *		
Exp. 2	4.7 ± 1.2 (24) **		4.5 ± 1.4 (42) **

(p<0.10), but not in Vipingo. In Vipingo, although tied together, *Diadema* were occasionally observed inhabiting different crevices. Therefore, the experiment may not have consistently measured the effect of sociality on predation rates at this site.

Comparisons of predation on different reefs

Survival of tethered *E. mathaei* in the 14 study sites indicated that predation was correlated with differences in sea urchin abundance and species composition. Population densities of sea urchins were negatively correlated with relative predation rate (Fig. 20). Species richness and diversity (Fig. 21) were highest with intermediate predation rates and with low to intermediate *E. mathaei* density. Where *E. mathaei* were dense, diversity and species richness were greatly reduced (Fig. 22). Where predation rates was reduced the absolute and relative importance of *E. mathaei* increased.

Relationship Between Living Communities and Substrate Cover and Complexity

Table 13 and 14 present the results of measuring substrate and cover diversity in different reefs. Large variance of measured variables indicates patchy distributions. Coral cover varied from 4.6% in Diani to 30% in Watamu. Protected and unprotected reefs
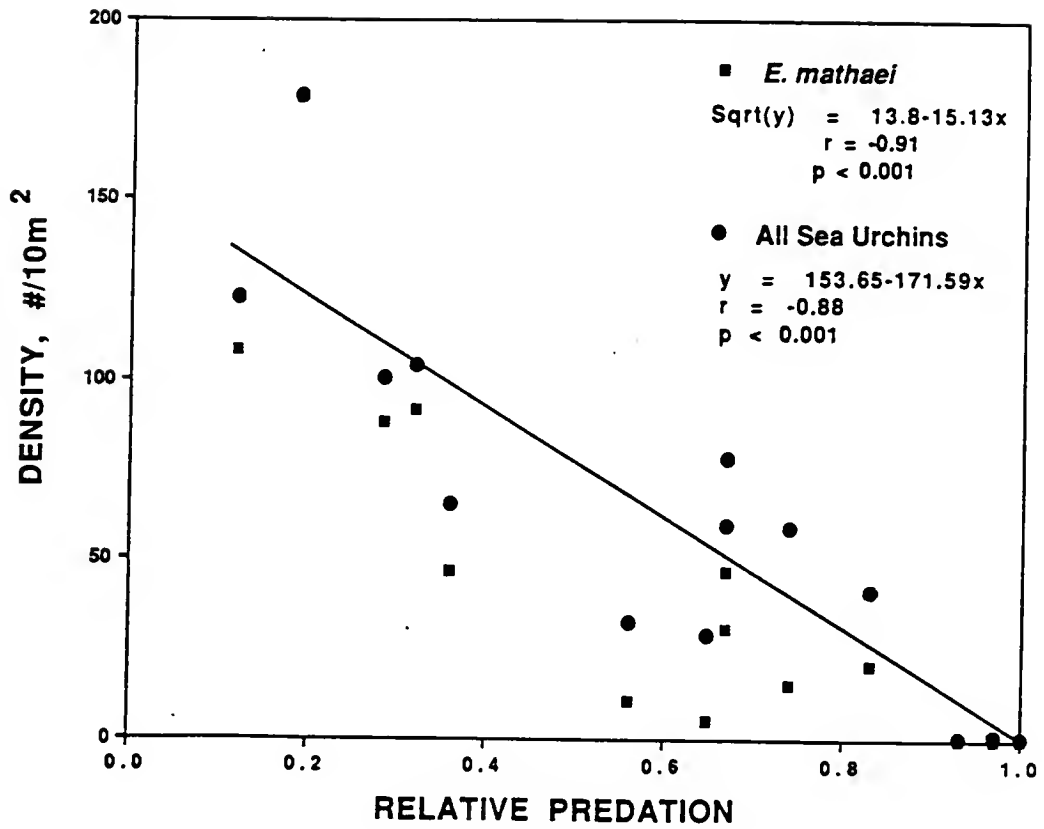
Fig. 20. Total sea urchin and *Echinometra mathaei* densities plotted against relative predation intensity at 14 sites.
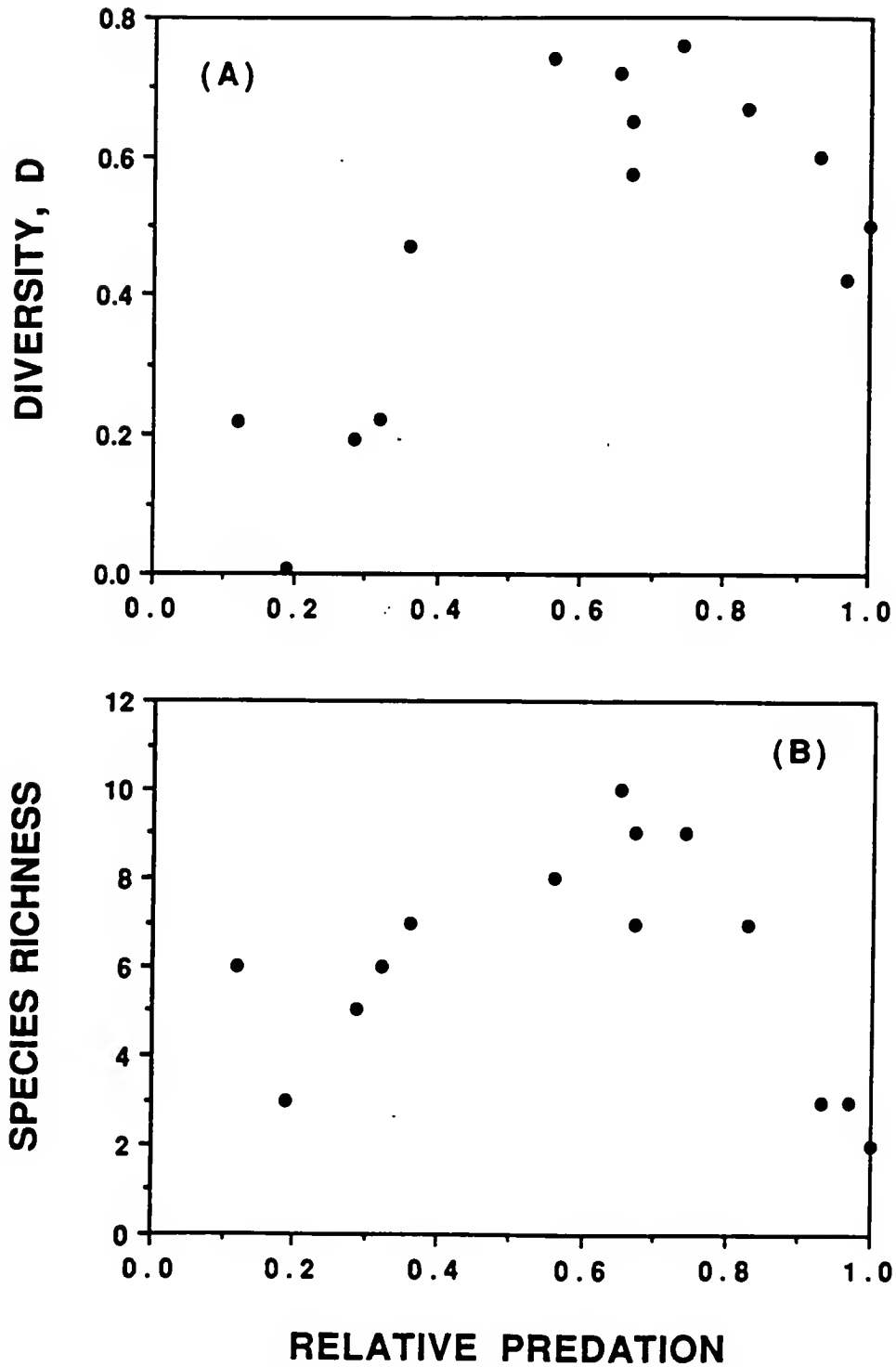
Fig. 21. Scatter-plots of species diversity (a) (Simpson's Index) and species richness (b) as a function of relative predation intensity on *Echinometra mathaei*.
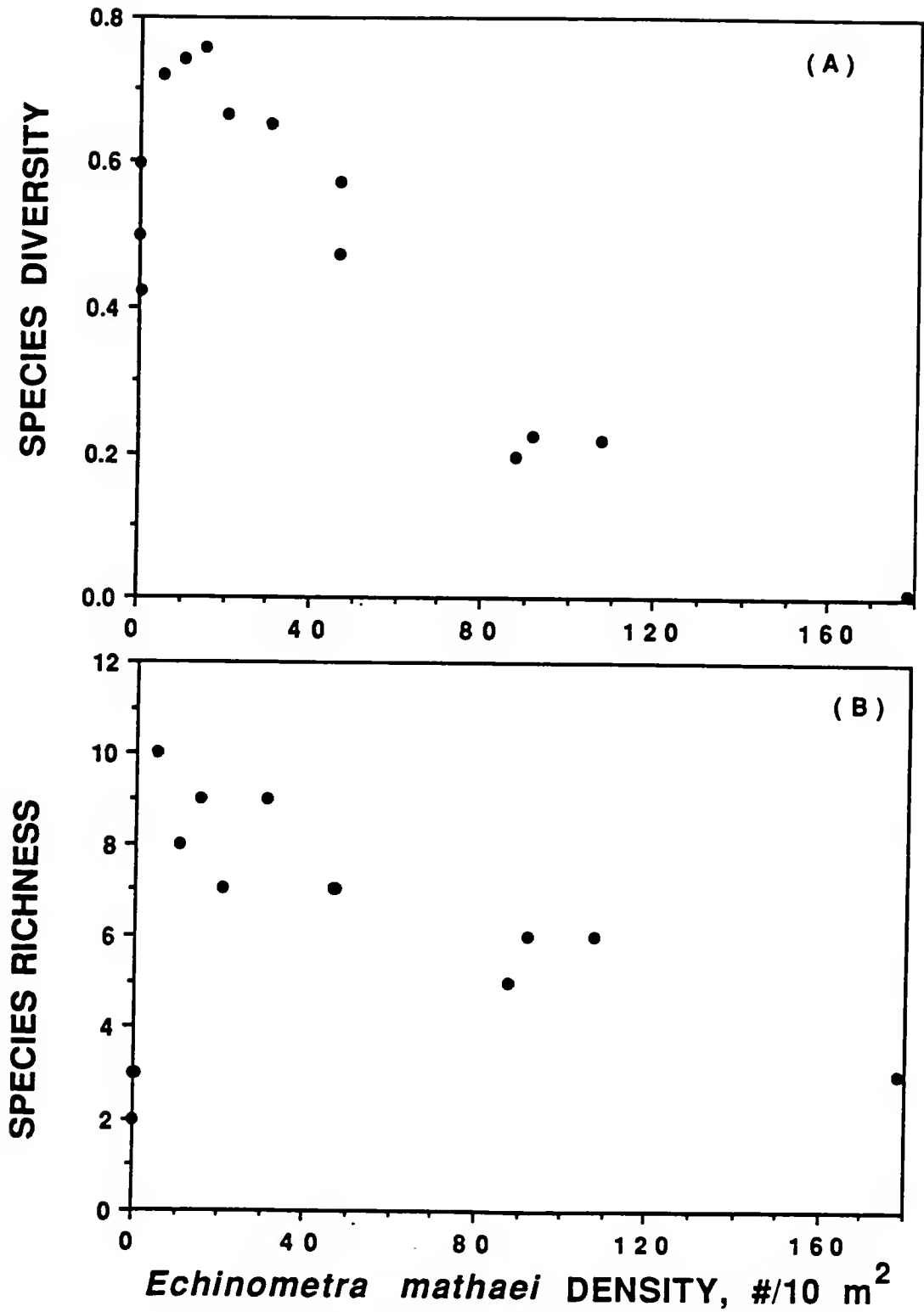
Fig. 22. (a) species diversity (Simpson's Index) and (b) species richness plotted against *Echinometra mathaei* density.

Table 13. Water depth at low tide, topographic complexity (rugosity), diversity of benthic organisms (Simpson's Index), and the percent cover (x ± S.D.), in the six locations. The significance level of a Kruskal-Wallis test of difference between reefs is provided.

	Malindi	Watamu	Vipingo	Kanamai	Bamburi	Diani	Kruskal-Wallis
Depth, m	0.8 ±0.3	1.1 ±0.2	0.4 ±0.2	0.4 ±0.1	1.1 ±0.3	0.6 ±0.1	
Topographic complexity	1.37 ±0.33	1.45 ±0.20	1.30 ±0.16	1.24 ±0.18	1.23 ±0.15	1.15 ±0.12	$p < 0.001$
Substrate diversity	0.82 ±0.0	0.78	0.59 ±0.1	0.67 ±0.0	0.53 ±0.1	0.60 ±0.0	$p = 0.07$
Percent Cover							
Hard coral	17.6 ±12.8	30.0 ±24.7	18.1 ±13.6	12.7 ±9.5	8.9 ±6.9	4.6 ±4.6	$p < 0.001$
Algal turf	27.6 ±20.5	19.7 ±17.5	58.6 ±19.8	44.3 ±15.4	66.3 ±14.8	54.7 ±22.2	$p < 0.001$
Calcareous algae	8.3 ±6.3	10.3 ±10.3	0.6 ±1.5	0.0 ±0.0	0.0 ±0.0	1.4 ±3.1	$p < 0.001$
Macro-algae	2.4 ±3.2	2.5 ± 2.9	2.8 ±4.2	0.9 ±2.4	2.4 ±3.0	1.5 ±1.9	$p < 0.05$
Seagrass	18.1 ±22.6	28.1 ±32.9	13.8 ±14.6	31.1 ±18.9	9.2 ±15.6	31.9 ±23.0	$p < 0.001$
Coralline algae	11.6 ±14.0	0.2 ±0.7	0.04 ±0.2	0.1 ±0.4	2.2 ±2.8	0.3 ±0.7	$p < 0.001$
Soft coral	1.4 ±2.4	0.0 ±0.0	1.9 ±3.0	1.8 ±3.6	3.0 ±3.8	0.8 ±1.2	$p < 0.006$
Coral sand	14.6 ±17.0	9.1 ±9.6	4.3 ±7.3	10.1 ±10.1	8.2 ±10.9	4.7 ±8.4	$p < 0.02$
Sponge	0.0 ±0.0	0.0 ±0.0	0.6 ±1.1	0.1 ±0.4	0.5 ±1.1	0.04 ±0.2	$p < 0.008$

Table 14 . Topographic complexity (rugosity), the percent cover (x ± S.D.), and diversity of benthic organisms in protected and in unprotected locations. The significance level of a Mann-Whitney U test of difference between protected and unprotected locations is provided.

	Protected	Unprotected	Mann-Whitney U test
Sites, n=	3	11	
Transects, n=	24	96	
Total transect length, m	240	960	
Topographic complexity	1.40 ± 0.06	1.24 ± 0.02	$p < 0.004$
Hard coral	22.23 ± 3.82	11.84 ± 1.12	$p < 0.005$
Algal turf	24.60 ± 3.97	55.24 ± 2.07	$p < 0.001$
Calcareous algae	8.21 ± 1.59	0.30 ± 0.10	$p < 0.001$
Macro-algae	2.45 ± 0.62	1.92 ± 0.32	NS
Seagrass	21.82 ± 5.45	20.91 ± 2.07	NS
Coralline algae	7.35 ± 2.52	0.67 ± 0.17	$p < 0.002$
Soft coral	0.86 ± 0.41	1.53 ± 0.28	NS
Coral sand	12.48 ± 3.00	6.89 ± 0.97	$p < 0.04$
Sponge	0.0 ± 0.0	0.42 ± 0.15	$p < 0.03$
Diversity, D	0.81 ± 0.01	0.59 ± 0.02	$p < 0.02$

(Table 14) differed in most categories. Protected reefs had higher coral cover, calcareous algae, coralline algae, and greater substrate diversity. Unprotected reefs had more algal turf. Topographic complexity was greater in protected reefs. A frequency distribution plot of topographic complexity measurements indicates a left-skewed or hierarchical distribution pattern (Fig. 23). Most of the substrate complexity was composed of small undulations with a few high relief areas usually created by old coral heads.

Because the calcium carbonate that provides the reef's structure and complexity is deposited by corals, topographic complexity and coral cover were closely related (Fig. 24). Total fish density was positively correlated with coral cover and complexity (Fig. 25a,b) while sea urchin abundance was negatively correlated (Fig. 26a,b). Therefore, total fish abundance correlated negatively (r=-0.82, p<0.05) with sea urchin abundance. An even stronger negative relationship was found between sea urchin and herbivorous fish abundance (Fig. 27).

A comparison of finfish families (Table 15) indicates that the Balistidae (triggerfish) were the only predators of sea urchins with densities higher in protected than in unprotected areas. Low population densities of sea urchins and high rates of removal of tethered sea urchins were strongly associated with high population densities of balistids (Fig. 28).
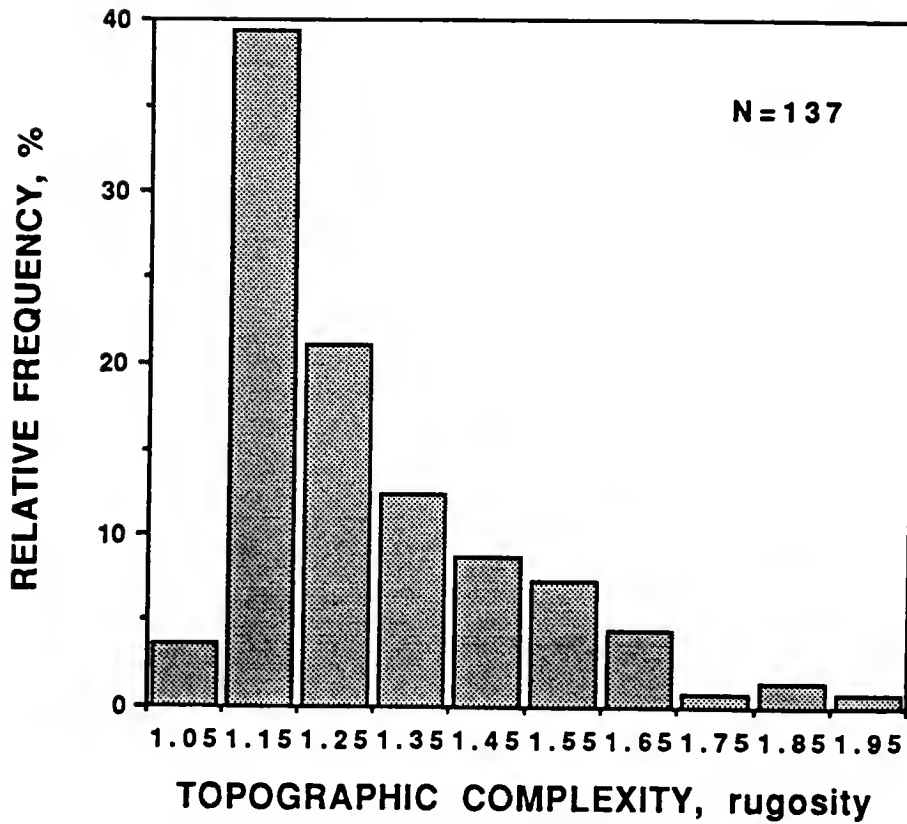
Fig. 23. Frequency distribution of topographic complexity measurements in all six Kenyan reef lagoons determined by the rugosity measurement. Rugosity is a straight line distance (10 m) divided the bottom contour distance transcended by the 10 m line.
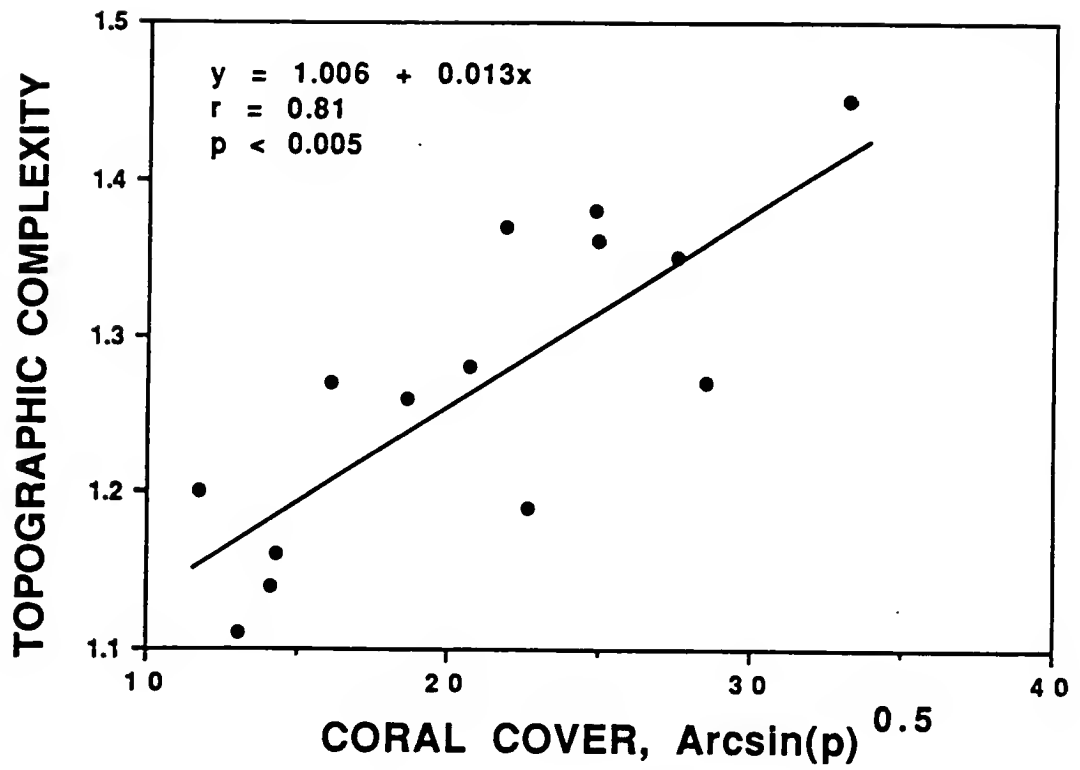
Fig. 24. Scatter-plot of coral cover versus topographic complexity within the 14 study sites.
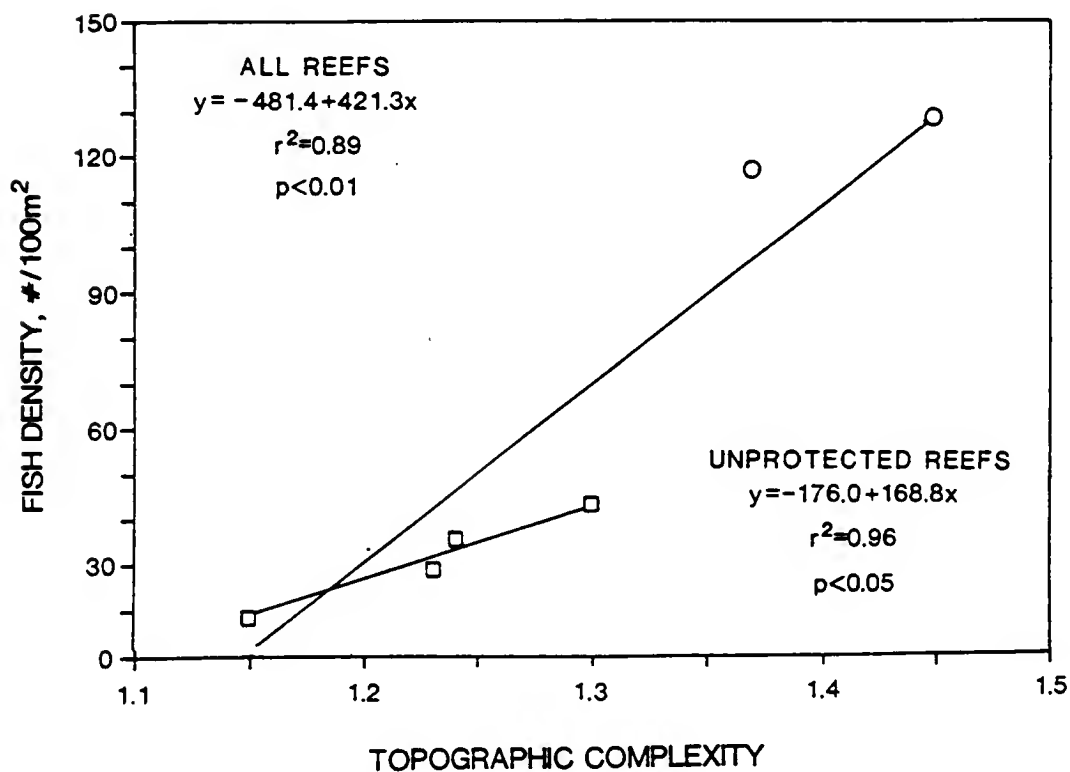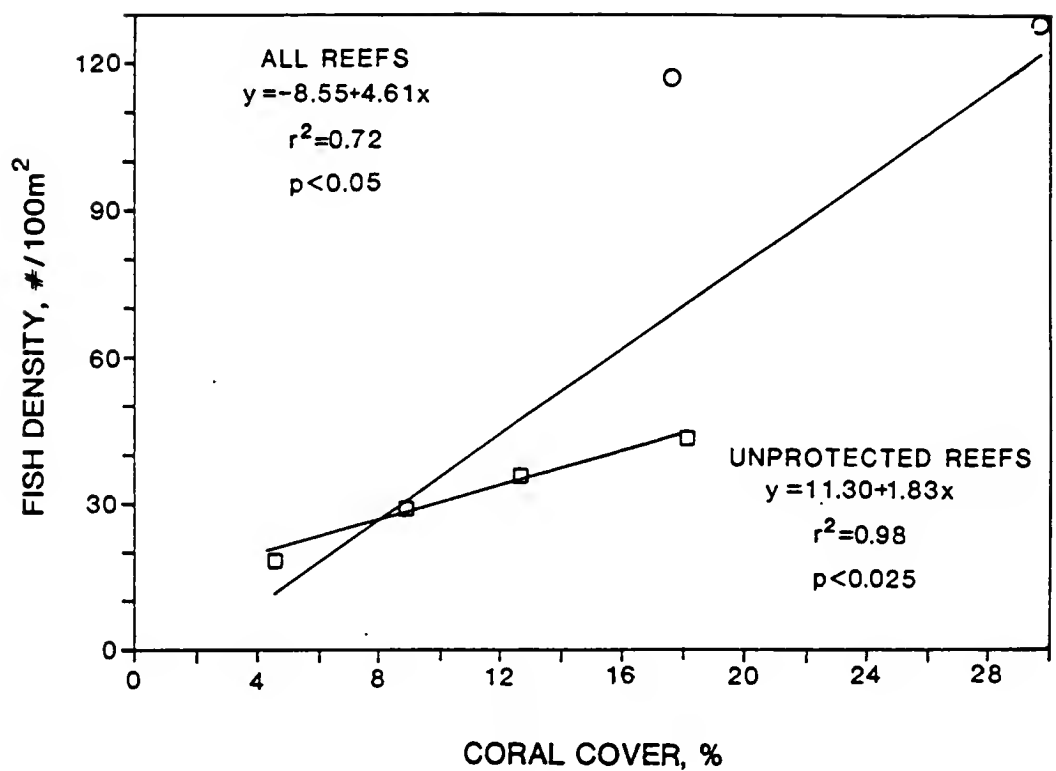
Fig. 25. Fish density and topographic complexity (a) (rugosity = straight line distance/ bottom contour distance), and coral cover (b). Regression analyses are included for all sites and the unprotected sites. Circles represent protected sites and squares unprotected sites.
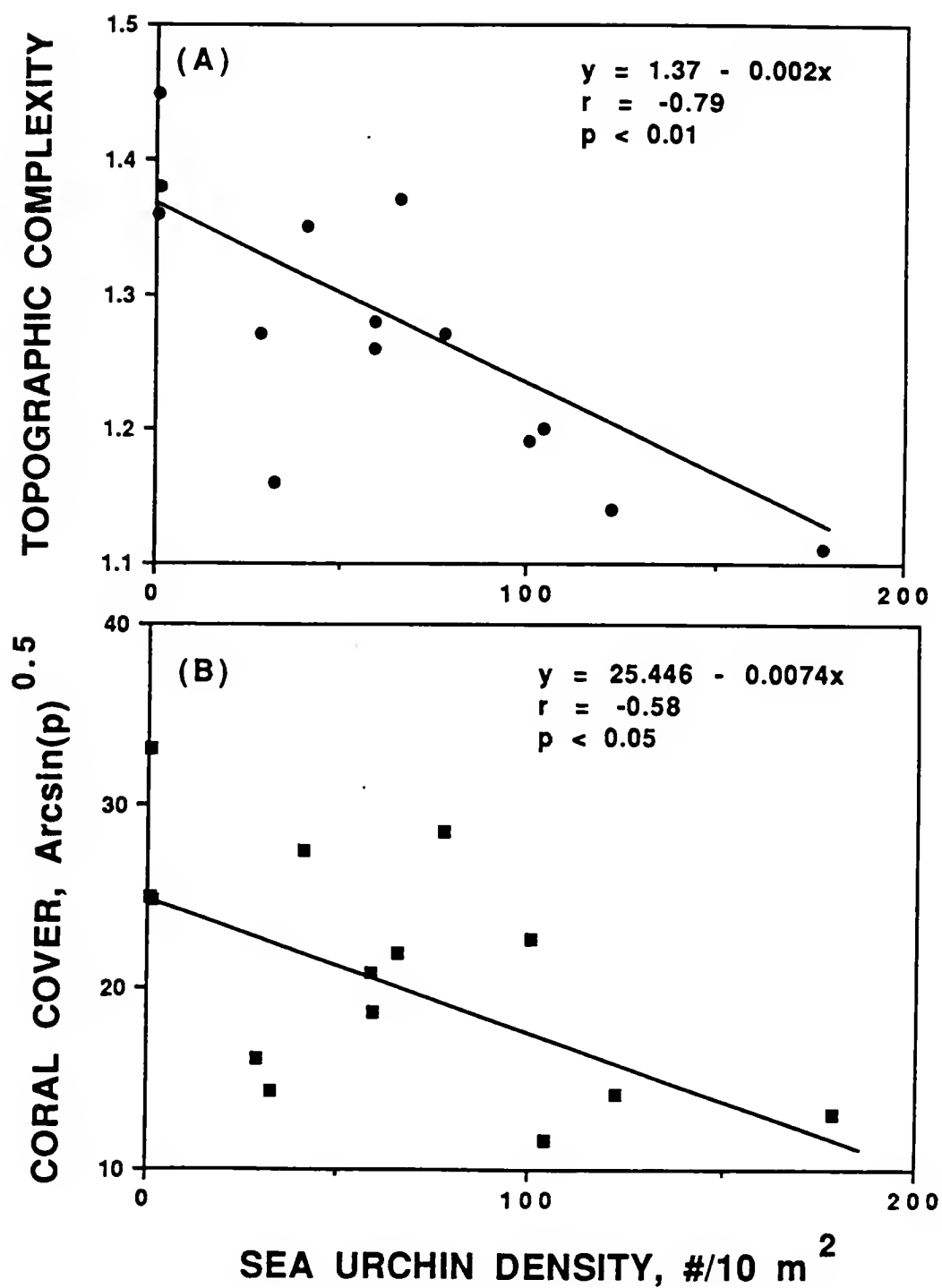
Fig. 26. (a) topographic complexity and (b) arcsine transformed coral cover (%) plotted against the total sea urchin density.
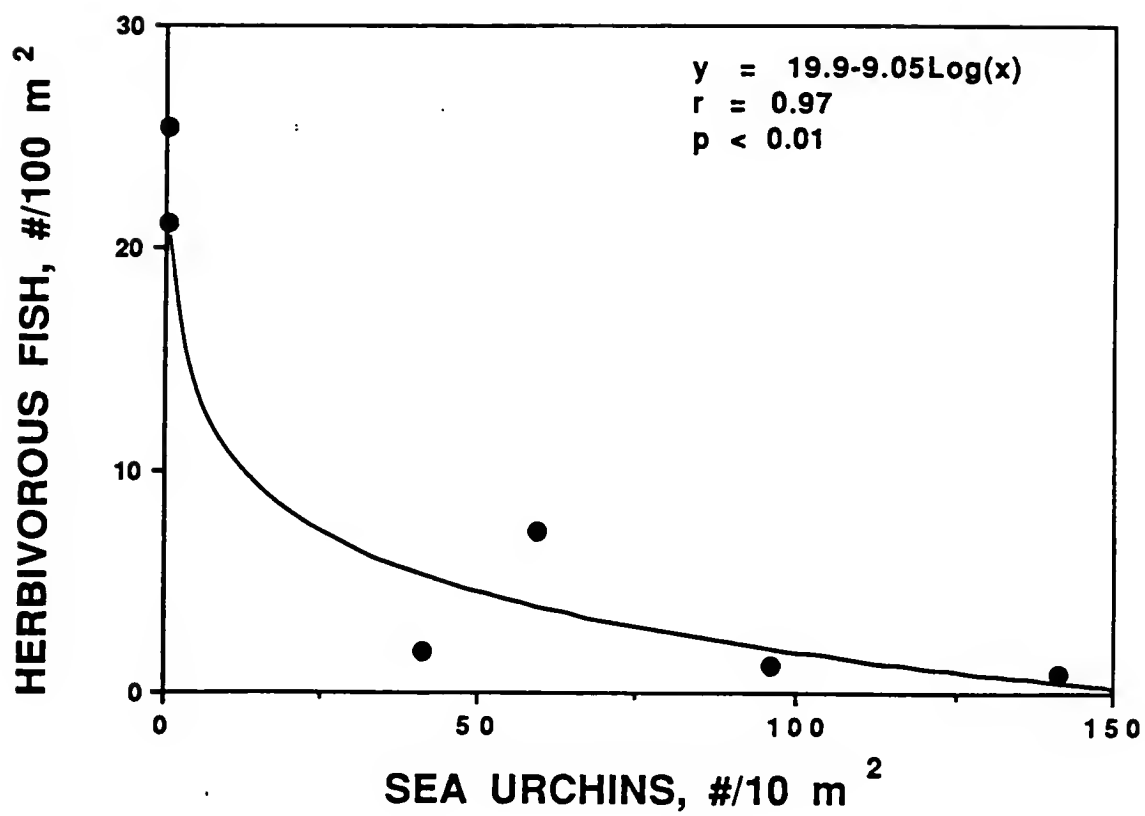
Fig. 27. Relationship between herbivorous fish (Scaridae and Acanthuridae) and sea urchin density.

Table 15. Comparison of fish that prey on urchins on 2 (n=8 transects) protected and 4 (n=21 transects) unprotected reefs. Values are densities (x $\pm$ s.em., #/100m^2) of the major sea urchin fish predator families and total fish (all families). Column 4 includes Mann-Whitney U-test of significance. NS = not significant.

	Protected Reefs	Unprotected Reefs	Mann-Whitney U-test
Labridae	11.4 $\pm$ 1.7	9.2 $\pm$ 1.9	NS
Balistidae	0.70 $\pm$ 0.14	0.07 $\pm$ 0.12	p<0.001
Diodontidae	0.03 $\pm$ 0.03	0.04 $\pm$ 0.02	NS
Lagocephalidae	0.03 $\pm$ 0.03	0.05 $\pm$ 0.03	NS
Total Predator Families	12.1 $\pm$ 1.7	9.3 $\pm$ 1.9	NS
Total Fish	121.4 $\pm$ 11.9	33.9 $\pm$ 4.3	p<0.001
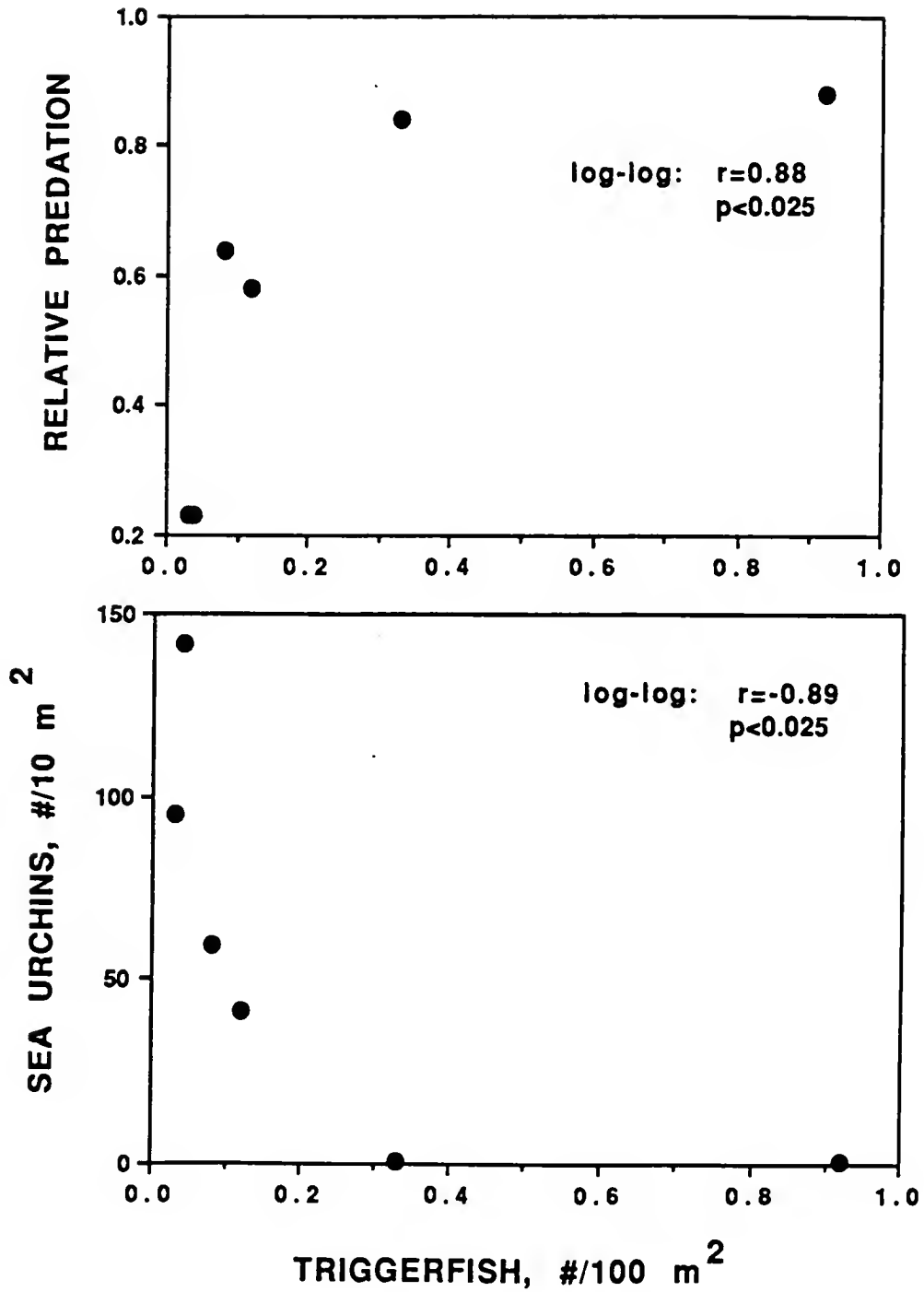
Fig. 28. Relationship between triggerfish and sea urchins in six Kenyan reef lagoons; (a) relative predation intensity on *Echinometra mathae;* .(b) total sea urchin density as a function of triggerfish density.

Differences in Trophic Structure

A trophic level analysis of protected and unprotected reefs (Fig. 29) suggests differences in principal energy flow pathways (algae-herbivorous fish-piscivores versus algae-sea urchins-triggerfish). Protected reefs had diminishing levels of biomass with increasing trophic level with most energy being transferred along the algae-herbivorous fish-piscivore pathway. Unprotected reefs had a large biomass "bulge" at the sea urchin herbivore level with little biomass in the form of herbivorous fish, piscivores or invertivores. The analysis used the average Kenyan reef algal biomass data taken from Moorjani (1978) for protected reefs and the average algal biomass in sea urchin-dominated reefs taken from literature values (see Table 24). The large variation from this average may be greatly affected by herbivore abundance not represented in this analysis.

Population Regulation of *Echinometra mathaei*

Density Manipulation Experiments

Population manipulation studies indicate variable responses to the addition and reduction of *E. mathaei* on experimental coral heads (Fig. 30). After leveling, population densities on population doubling experiments in Diani and Kanamai were not significantly different from those in controls. However, population densities were
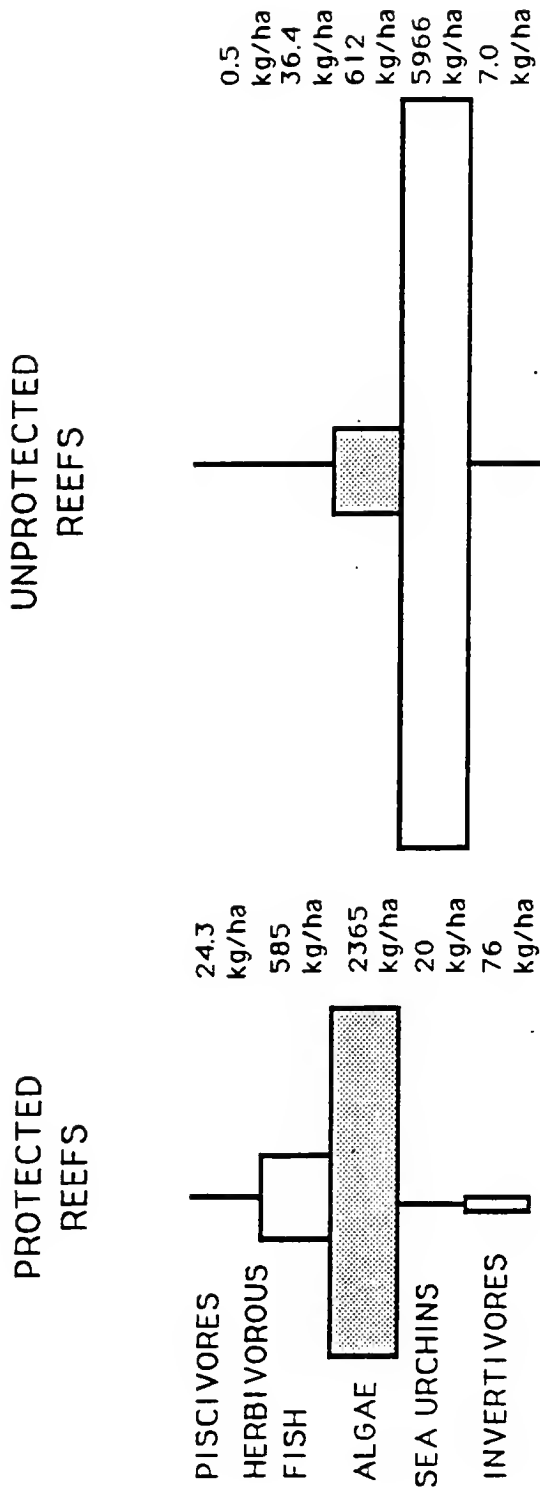
Fig. 29. Comparison of trophic biomass pyramids of protected and unprotected reefs. Patterns suggest that two alternate pathways exist (algae-herbivorous fish-piscivores and algae-sea urchin-predators of invertebrates). Algal data from Moorjani (1978) for protected reefs and literature values (Table 24) for unprotected reefs.
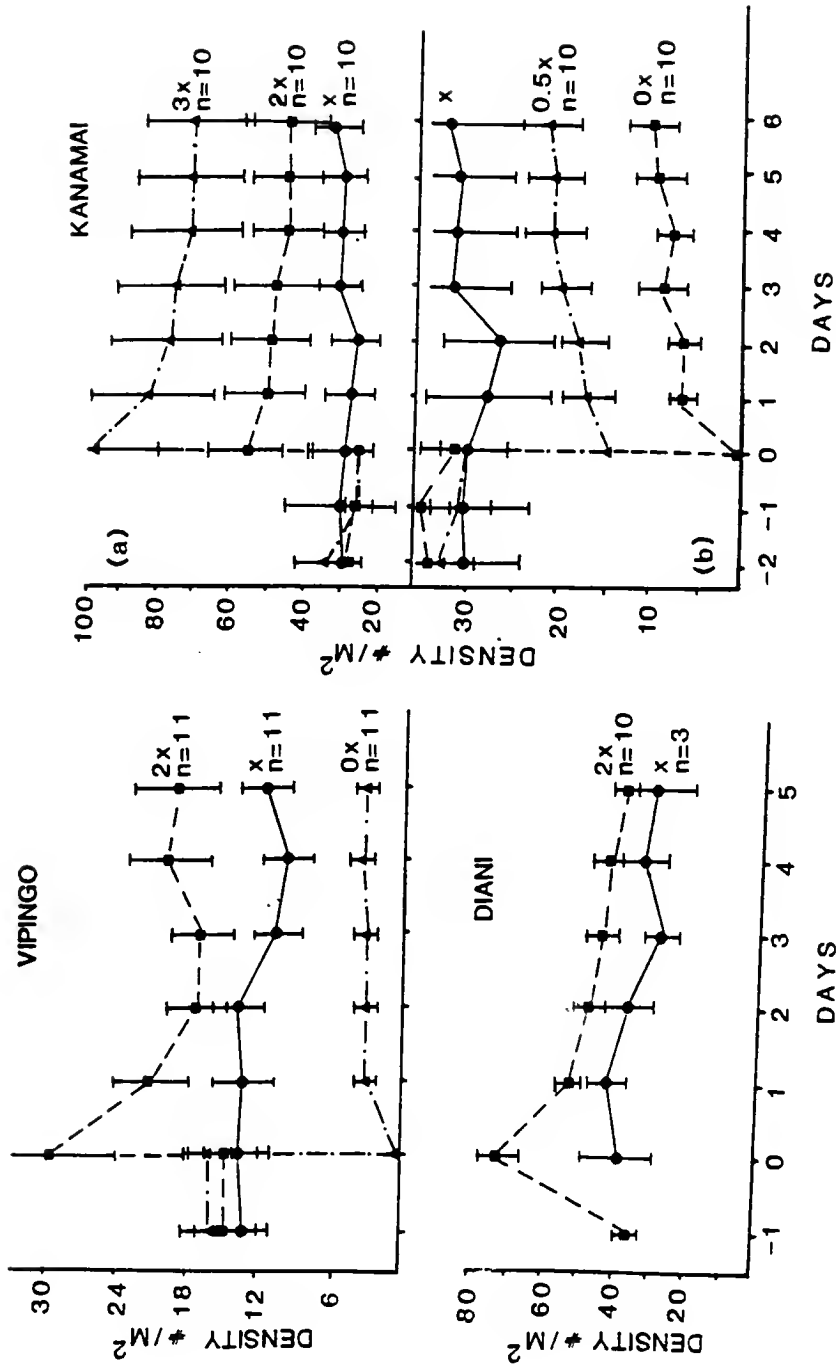
Fig 30. Population densities of *Echinometra mathaei* after density manipulation experiments were undertaken in Kanamai, Vipingo and Diani. Kanamai (a) urchins added; (b) urchins removed; 3x= density tripled; 2x=density doubled; x = control density, 0x all urchins removed, n = sample size. Bars represent 1 standard error of the mean (s.e.m.).

significantly higher for the Vipingo doubling experiments (t-test, p<0.05) and the Kanamai tripling experiment (t-test, p<0.01). Densities after reduction experiments were followed by small population recoveries but were significantly lower (t-test, p<0.05) than control coral head population densities.

In order to determine the degree of population change after experimental manipulations, plots of initial density versus the change in density were created. Changes in density were significantly correlated with initial density (Fig. 31) but differed depending on whether individuals were added or removed from coral heads. Slopes were significantly less (t-test, p<0.01) than 1, indicating changes from initial densities. A slope of 0.73 indicated an approximately 75% population adjustment after urchin additions. Population recovery after density reductions was less with a small slope of 0.15. After treatments, the population density was a function of both the site and the experimental manipulation. Tagged individuals (Fig. 32) left coral heads at a significantly greater rate (t-test, p<0.01) than control individuals. In density increase experiments, density changes could most frequently be attributed to added individuals. However, the decrease in control densities may have resulted from some natural movement, predation or paint mark losses.

Body sizes were not different (t-test) before and after addition experiments (Fig. 33) and had similar unimodal frequency distributions of body size. Body sizes were significantly smaller (Mann-Whitney U-test, p<0.01) after reduction experiments, and test size frequency distributions were randomly distributed.
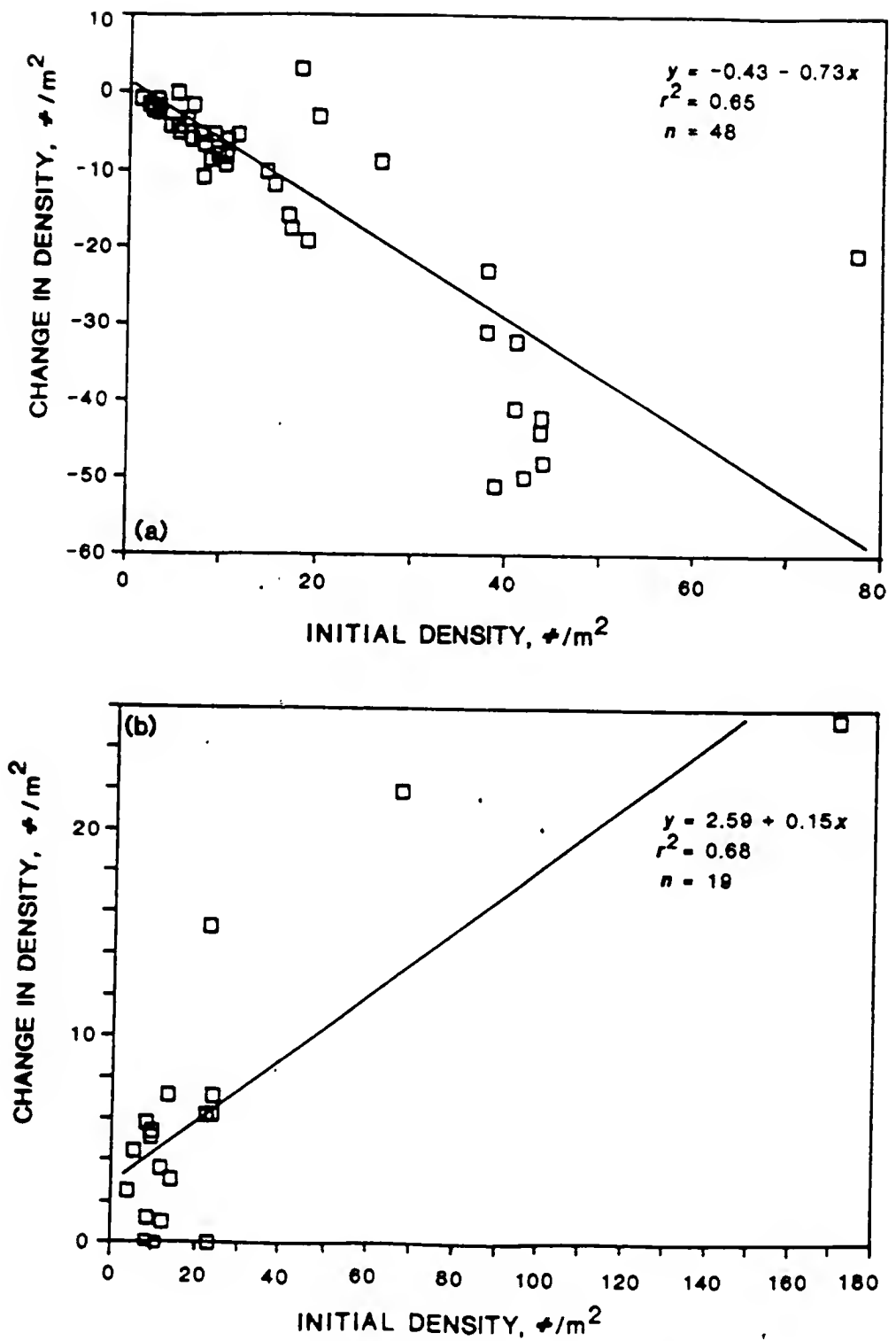
Fig 31. *Echinometra mathaei* density changes 5 days after density manipulations as a function of the initial densities combining all sites for (a) doubling and (b) total reduction experiments.
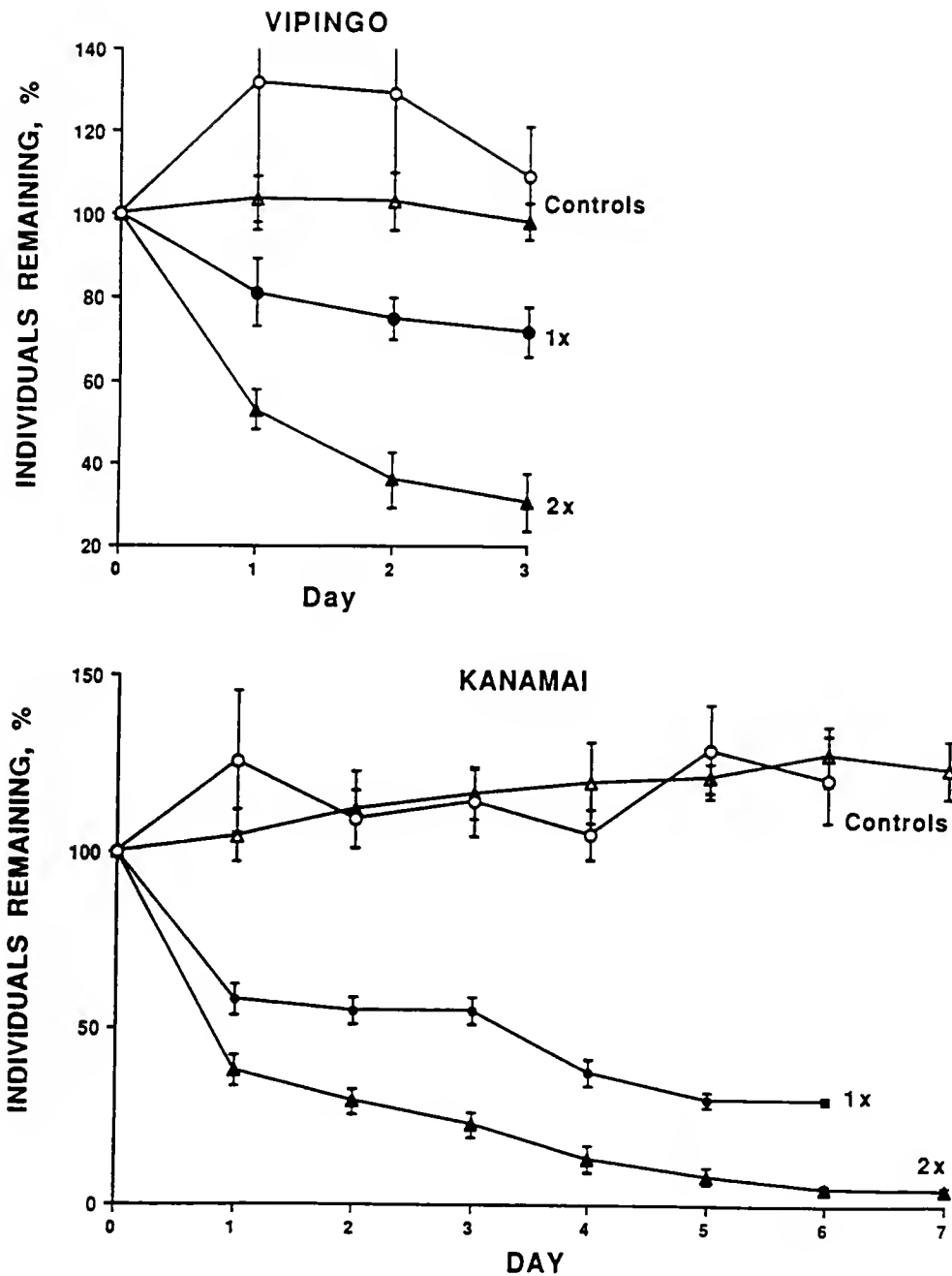
Fig 32. Percent *Echinometra mathaei* individuals remaining on coral heads after experiments. Includes controls where densities were left unchanged and doubling sea urchin densities (2x). Added individuals are represented by solid symbols. Original inhabitants are represented by open symbols. Controls are represented by circles and density doubling experiments are represented by triangles. Bars represent 1 standard error of the mean., sample size =10 for each category.
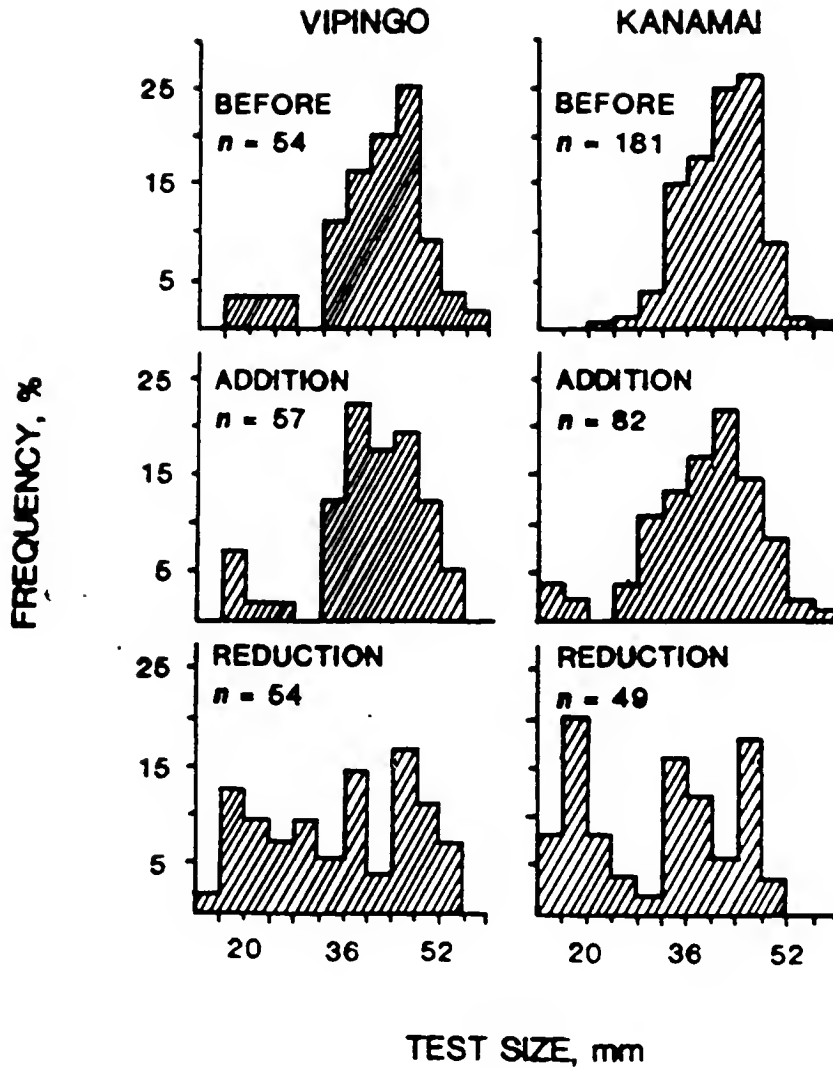
Fig 33. Frequency distributions of *Echinometra mathaei* body sizes (tests) before and after total sea urchin removal and population density doubling experiments on Vipingo and Kanamai coral heads. Addition, population doubled; reductions, all urchins removed. n= sample size.

In the population doubling experiment added animals had greater mortality than original inhabitants and control individuals (Table 16). Differences between controls and experiments were not large. The mortality that was not attributable to predation, was possibly caused by individuals falling off coral heads and hanging themselves on the tethers. More than 85% of the mortality was due to predators. On experimental population density increases, predation occurred on 28.6% of the Kanamai and 32.1% of the Vipingo urchins. On controls, predation occurred on 5.7% and 14.3% of the Kanamai and Vipingo urchins.

Tests of agonistic behavior indicate significantly greater (G-test, $p<0.001$) burrow defense in Vipingo than Diani (Table 17). Within Vipingo more than 80% of the encounters resulted in fights, which in most cases resulted in the expulsion of intruders. Most of the animals in the Vipingo coexistence category (n=6 or 17%) were still pressed against each other for more than the allotted time. Diani individuals were quiescent and 70% of the interactions resulted in coexistence. Considering that we selectively used individuals from crevices or burrows, and this was a small percent of the total population, the level of agonistic behavior in Diani is probably even lower than indicated by this experiment.

Morphological and Physiological Measurements

Results of physiological experiments and morphological measurements suggest distinct differences between populations and

Table 16. Survival rates in days (x ± S.D.) for a three-day experiment to determine the effect of doubling populations of *Echinometra mathaei* on mortality. A maximum index value of 3.0 indicates that all individuals survived the duration of the 3 day experiment. Survival is given for original inhabitants, added individuals (recruits), and for control animals in which the coral head population was not doubled. Data are presented for two different reef lagoon sites. Mortality from predation was distinguished by the presence, absence, or condition of the carcass. Categories of total mortality and predation are included as well as the percentage of mortality due to predation in each experimental group. Mann-Whitney U-test of recruits versus control survival rates.

	Vipingo				Kanamai			
	Original Inhabitants	Additions (Recruits)	Controls	Mann-Whitney U-test	Original Inhabitants	Additions (Recruits)	Controls	Mann-Whitney U-test
n=	52	56	56		49	49	49	
Mortality	±0.19	±1.19	2.66 ±0.72	p<0.01	2.41 ±1.04	2.51 ±0.87	2.94 ±0.24	p<0.05
Predator Induced Mortality	2.96 ±0.19	2.38 ±1.12	2.75 ±0.61	p<0.01	2.47 ±1.00	2.51 ±0.87	2.94 ±0.24	p<0.05
Predator Induced, % of total	100	68.4	62.5		86.7	100	100	

Table 17. Results of intraspecific competition experiment undertaken within Vipingo and Diani reef lagoons. Individuals were placed at *Echinometra mathaei* burrow entrances and interactions were recorded to determine interaction type and outcome of encounters. Absolute number of observations and percentages (in parentheses) are given in each category.

Vipingo
Total n=35

Fight
n=29(82.9)
Host Left   Intruder Left   Coexist
n=0(0)   n=23(65.7)   n=6(17.1)

No Fight
n=6(17.1)
Contact   No Contact
n=4(11.4)   n=2(9.4)
Host left   Intruder Left   Coexist
n=0(0)   n=4(11.4)   n=0(0)

Diani
Total n=30

Fight
n=4(13.3)
Host Left   Intruder Left   Coexist
n=0(0)   n=3(10.0)   n=1(3.3)

No Fight
n=26(86.7)
Contact   No Contact
23(76.7)   n=3(10.0)
Host Left   Intruder Left   Coexist
n=1(3.3)   n=1(3.3)   n=21(70.0)

responses to various conditions. Respiration rates were low, typical of sea urchins (Binyon 1972, Shick 1983). Starvation resulted in lowered respiration rates (Fig. 34). Fed sea-urchins consumed 0.58 $\pm$ 0.22 (x $\pm$ S.D., n=14 days) grams of cabbage per individual per day, which from combustion experiments is equivalent to 48 mg of dry organic material/day.

Gonad sizes of starved and fed individuals were both low in comparison with field populations (Table 18). *E. mathaei* in Diani had significantly lower respiration rates, gonad weights, and gonad indices but a larger Aristotle's lantern index values (Table 19). The Diani gonad index was 35% smaller and Aristotle's lantern index 25% larger than Vipingo individuals.

Diani individuals had relatively longer and heavier Aristotle's lanterns than Vipingo individuals. The intercepts of the best-fit lines for both comparisons were significantly greater for animals on Vipingo (t-test, $p<0.01$; Fig. 35). The slope of the body length-lantern length comparison was significantly greater (t-test, $p<0.01$) for animals in Vipingo. Comparisons within sites at two different times were not significantly different with the exception of respiration rates on Diani. Diani individuals had greater variance in Aristotle lanterns and respiration. Respiration rates of starved aquarium individuals were better correlated with weight (y=-0.43 + 0.04x, r=0.56, $p<0.005$) than were fed individuals (y=0.08 + 0.03x, r=0.35, $p<0.05$). Starved individuals were typically inactive, whereas fed individuals displayed variable activity while in experimental jars, which may account for differences.
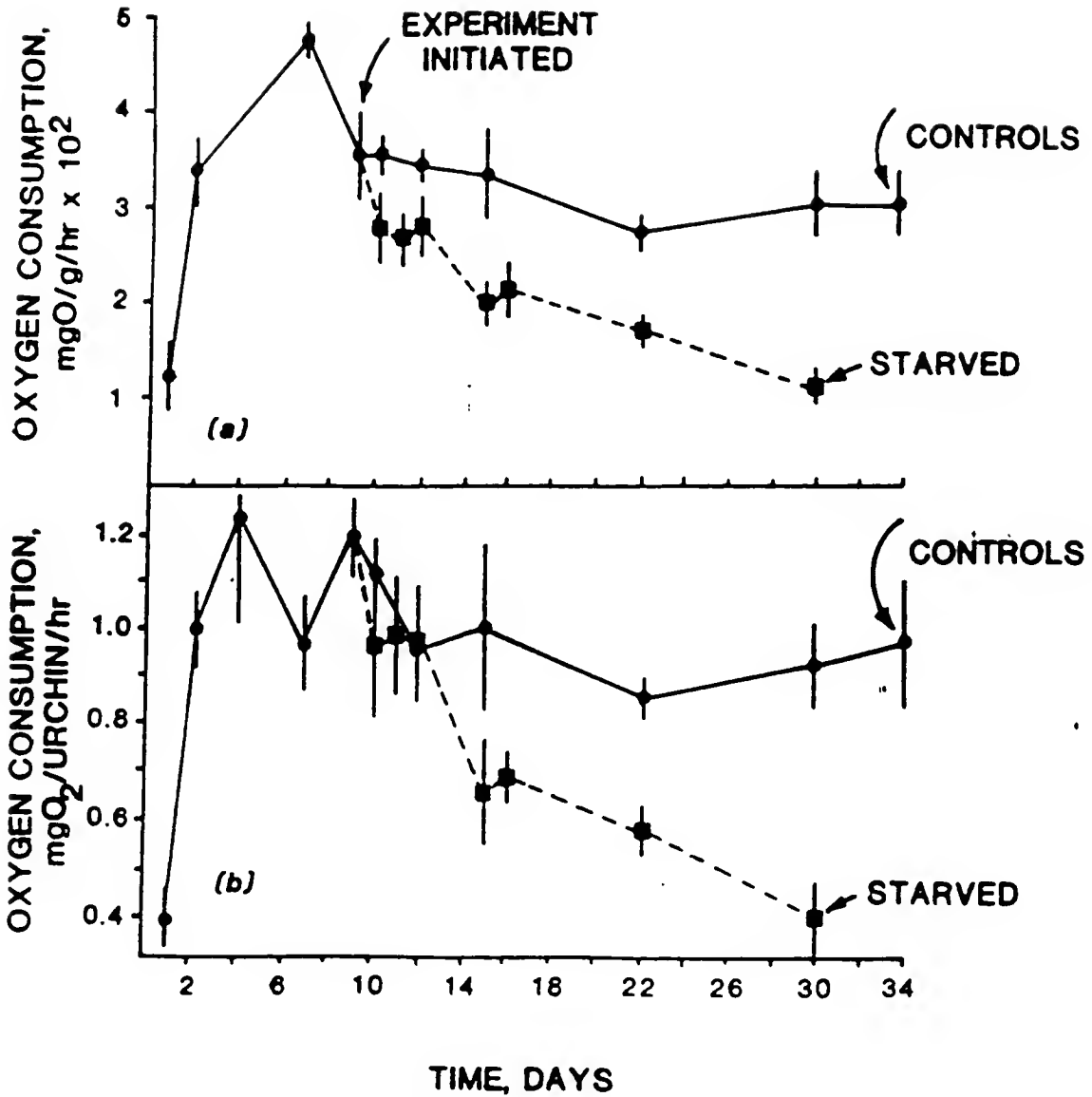
Fig 34. Respiration rates of fed and starved *Echinometra mathaei* (a) on a per gram basis and (b) whole individuals before and after removal of food on the ninth day of the experiment. Bars represent ±1 standard error of the mean.

Table 18. Mean respiration rates (x ±S.D.) and gonad indices for *Echinometra mathaei* at Vipingo and Diani during July 1988. Gonad weight in grams wet weight; gonad index (wet gonad weight/wet body weight x100), lantern indices (wet Aristotle's lantern weight/wet body weight x 100) and statistical tests for comparisons between individuals collected during two time intervals (t1 and t2). Respiration rates of starved and fed individuals in aquariums taken for the period 10 to 34 days after the experiment's initiation. Gonad indices calculated after termination of experiment (34 days).

	Vipingo t1	t2	total	Within Site t-test	Diani t1	t2	total	Within Site t-test	Between Site t-test	Aquarium Feed	Starved	Total ANOVA
Respiration Rate mgO2/g/hr x 100	4.81 ±0.92	4.66 ±0.68	4.73 ±0.77	NS	4.71 ±1.17	2.84 ±0.55	3.77 ±1.31	p<0.005	p<0.025	3.27 ±0.84	2.24 ±0.78	p<0.0001
n=	6	6	12		6	6	12			36	41	
Gonad Weight, g	2.07 ±1.24	1.88 ±1.44	1.98 ±1.34	NS	1.01 ±0.73	1.06 ±0.71	1.03 ±0.72	NS	p<0.001	0.54 ±0.26	0.40 ±0.20	p<0.0001
n=	20	16	36		20	20	40			9	10	
Gonad Index	5.06 ±1.87	4.65 ±2.72	4.88 ±2.26	NS	2.91 ±1.84	3.17 ±1.94	3.04 ±1.87	NS	p<0.0005	1.77 ±0.82	1.59 ±0.83	p<0.0001
n=	20	16	36		20	20	40			9	10	
Wet body weight, g	20.4 ±3.7	44.1 ±9.1			23.5 ±6.0	32.0 ±5.5				29.8 ±3.2	33.1 ±5.1	

Lantern Index	6.38	8.00	p<0.0005
	±0.67	±1.09	
n=	30	31	

Table 19. Characteristics of *Echinometra mathaei* on Vipingo, Kanamai, and Diani reefs including adults and recruits (test size < 1.5 cm) densities (x $\pm$ S.D./1m^2), test sizes, wet weight biomass, dry organic matter biomass, gut indices and coefficents for correlations of adult and recruit densities in the 1 m^2. Kruskal-Wallis or F-test comparions included. NS=not significant, * = p<0.05, ** = p<0.005 and *** = p<0.001.

	Vipingo	Kanamai	Diani	Statistical Signficance
n=	25	25	50	
Adults	5.96 ±4.10	·11.28 ±8.43	22.84 ±19.43	***
Recruits	1.20 ±1.26	1.08 ±1.44	0.90 ±1.43	NS
Test Size	41.1 ± 13.3	41.0 ± 8.1	38.5 ±6.7	*
n=	36	50	105	
Biomass g/m^2	217	408	700	
Dry Organic Matter g/m^2	10.9	23.7	40.6	
Adult-Recruit r=	0.50 *	0.14 NS	0.56 **	
Gut Index	8.04 ± 3.9	7.69 ± 4.5	5.45 ± 1.9	**
n=	(20)	(29)	(20)	
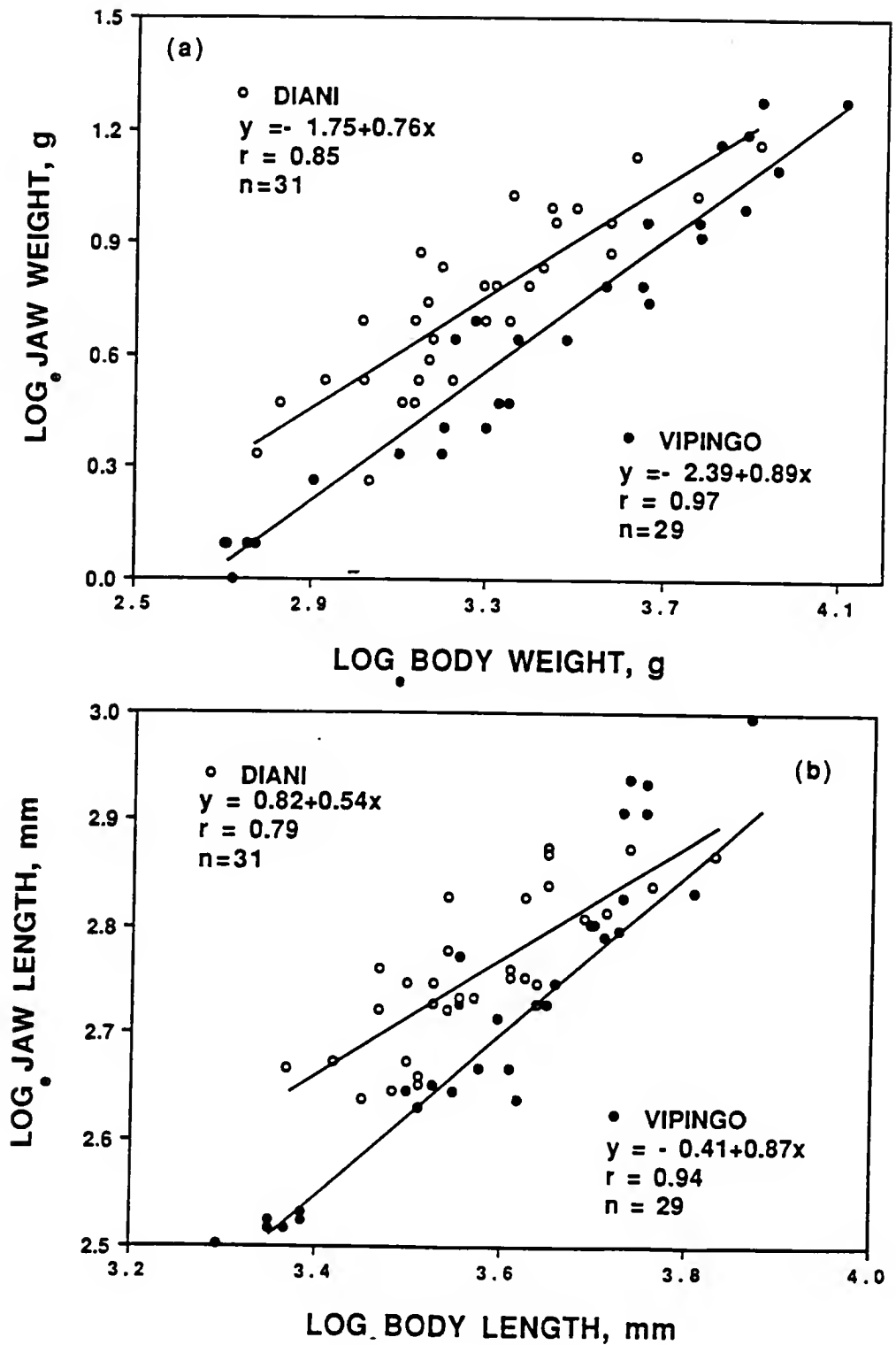
Fig 35. Allometric relationships between structures of *Echinometra mathaei* on Vipingo and Diani reefs. Aristotle lantern weights as a function of body weights (a) and Aristotle lantern lengths as a function of average body lengths (b).

Long Term Population Changes

Population studies indicate that *E. mathaei* densities on Kanamai and Diani increased by 9.6 and 5.4 individuals/m^2 respectively between 1985 and 1989 with a large increase in 1987 (Fig. 36a). Vipingo's density of *E. mathaei* was more constant. Test sizes decreased by only 3.0 mm in Diani between 1985 and 1989 (t-test, p<0.01). Nonetheless, there was little indication of reduced test size with increasing sea urchin density (Fig. 36b). Measurements on recruitment (Table 19) show similar densities (about 1/m^2) for the 3 study sites. In Vipingo and Diani densities of recruits were weakly but positively correlated with adult densities (Table 19). In Diani, hard substrate decreased and seagrass which is associated with coral sand increased by 10% between 1985 and 1988 (Table 20) .

Calcium Carbonate Balance

Sea urchin gut contents were inversely proportional to urchin density. Vipingo urchins had the fullest guts followed by those on Kanamai and lastly those on Diani (Fig. 37a). Rates of total and calcium carbonate gut evacuation were similar for all three reefs (Fig. 37b). Slopes of the calcium carbonate defecation rate plotted against time is assumed to equal the hourly substrate bioerosion rates. The average bioerosion for all sites was 0.415 g/urchin/day. The fraction of calcium carbonate in the gut increases with the urchin population
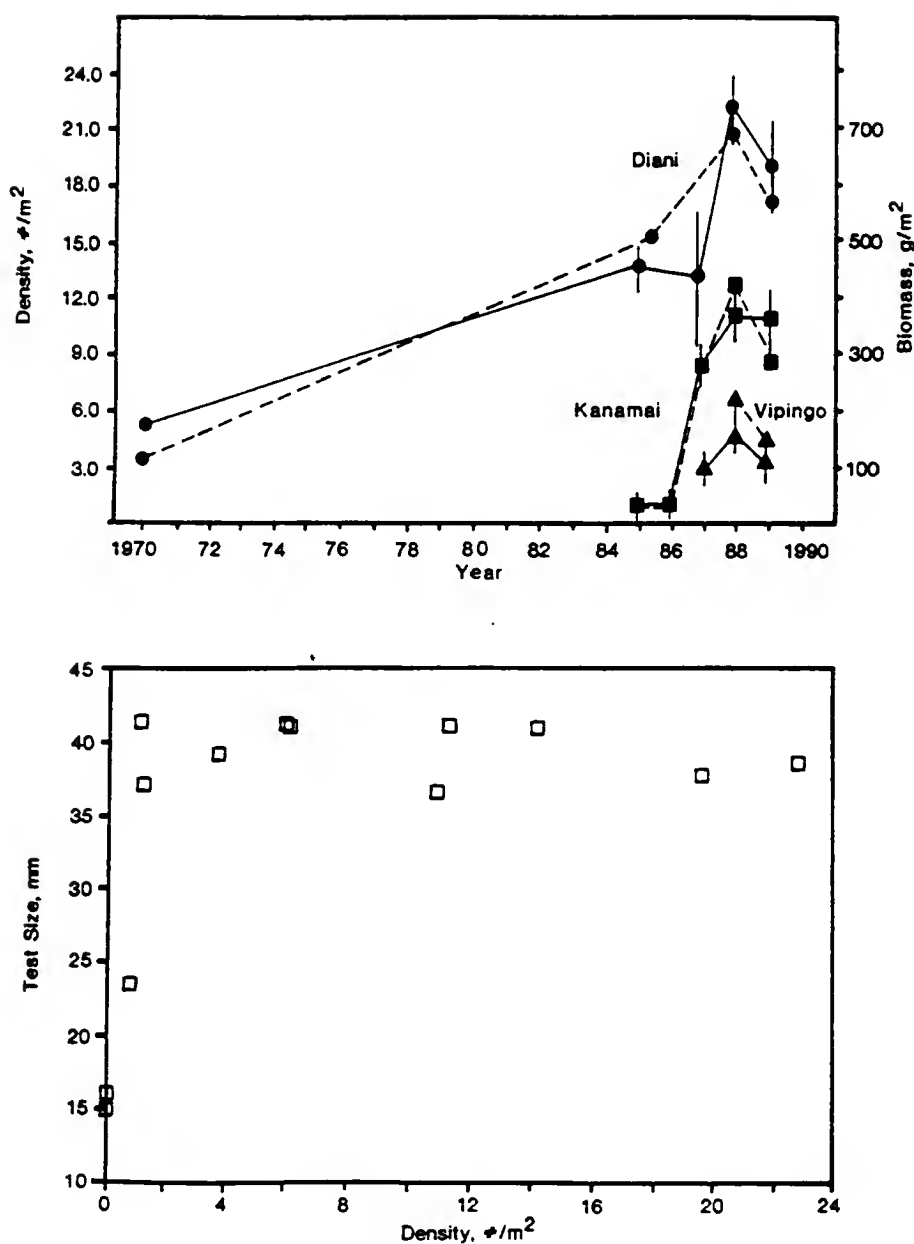
Fig 36. Characteristics of *Echinometra mathaei* on Kenyan reefs from 1985 to 1989. Change in population density on three reefs (a). Data prior to 1988 are taken from Khamala (1971), McClanahan and Muthiga (1988) and this study. Bars represent ±2 standard errors of the mean. The relationship between sea urchin density and body (test) size (b).

Table 20. Comparison of mean substrate cover (x ± S.D.) within the Diani reef lagoon for two years (1985 and 1988) based on running averages (n=29) for 90 quadrats per year. Hard substrate was dead coral usually covered by algal turf.

Cover Type	1985	1988	t-test
Hard Substrate	43.1 ± 18.0	34.6 ± 15.6	p<0.05
Seagrass	26.8 ± 14.1	36.3 ± 15.4	p<0.01
Coral Sand	30.1 ± 12.4	27.8 ± 9.2	NS
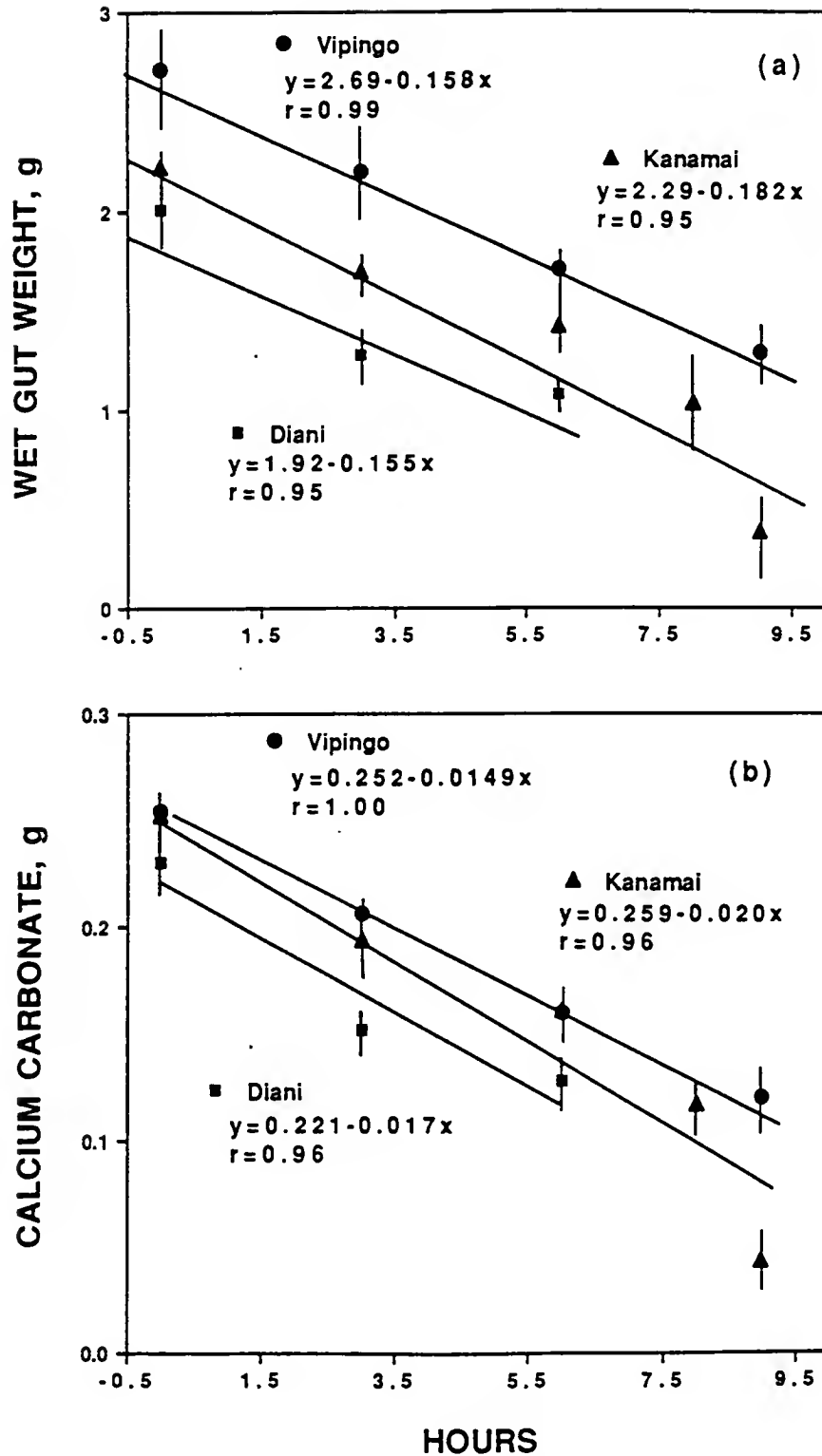
Fig. 37. Gut evacuation rates of *Echinometra mathaei* on three Kenyan reefs: (a) total weights, and (b) calcium carbonate as a function of the time urchins were removed from the substrate.

density (Fig 38). Nonetheless, there is no indication that bioerosion rates increase with urchin density, since gut turnover rates are constant and absolute quantities of calcium carbonate are similar at different densities.

The gross calcium carbonate deposition rates were estimated from coral cover (Table 13) and the equation given in the Methods (Calcium Carbonate Deposition). Bioerosion rates were estimated by combining urchin density and the bioerosion rate per urchin. Net calcium carbonate balance for the six Kenyan reef lagoons suggests net gains in calcium carbonate in all sites except Diani (Fig. 39). Kanamai was very close to neutral.

Calculations do not include deposition due to other organisms such as calcareous and coralline algae or erosion due to fish and other invertebrates or the physical erosion of the reef substrate. The greatest quantities of coralline and calcareous algae are in the protected reef areas (Table 13), and therefore calcium carbonate deposition may be underestimated in the protected reefs. Physical erosion is likely to be small in most reef lagoons due to reduced physical forces at work there but may contribute some to the total erosional budget. Comparison of data for protected and unprotected sites (Fig. 40) suggests that protected reefs have large net calcium carbonate accretion rates whereas unprotected reef lagoon losses due to urchins are close to gains.
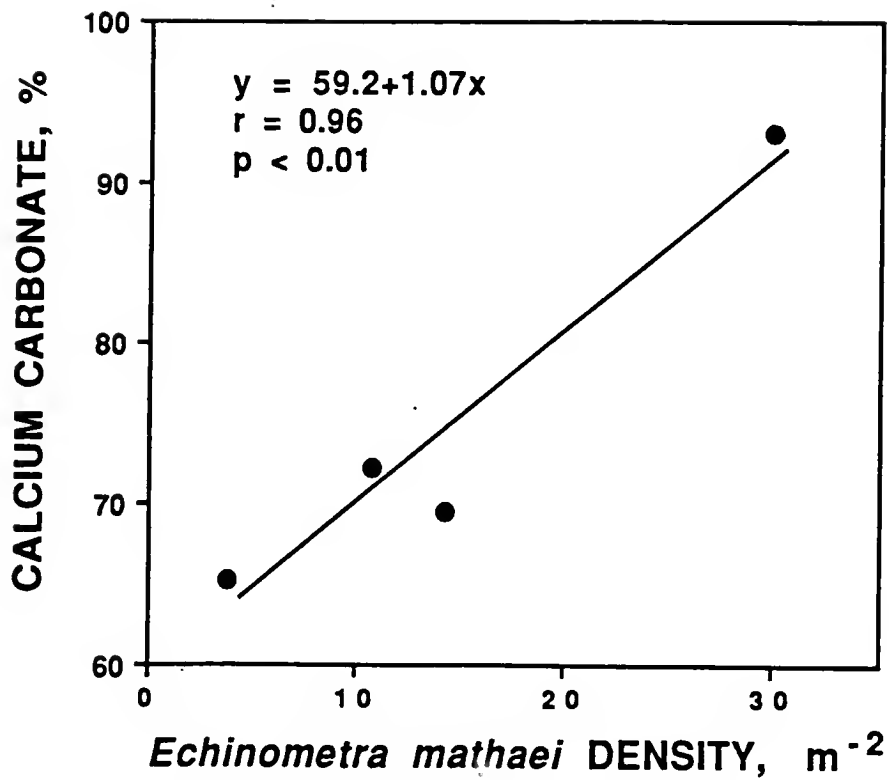
Fig. 38. Percent calcium carbonate in the gut content of *Echinometra mathaei* as a function of their population density. The graph includes data from two other published studies (Muthiga and McClanahan 1987 and Downing and El-Zahr 1987).
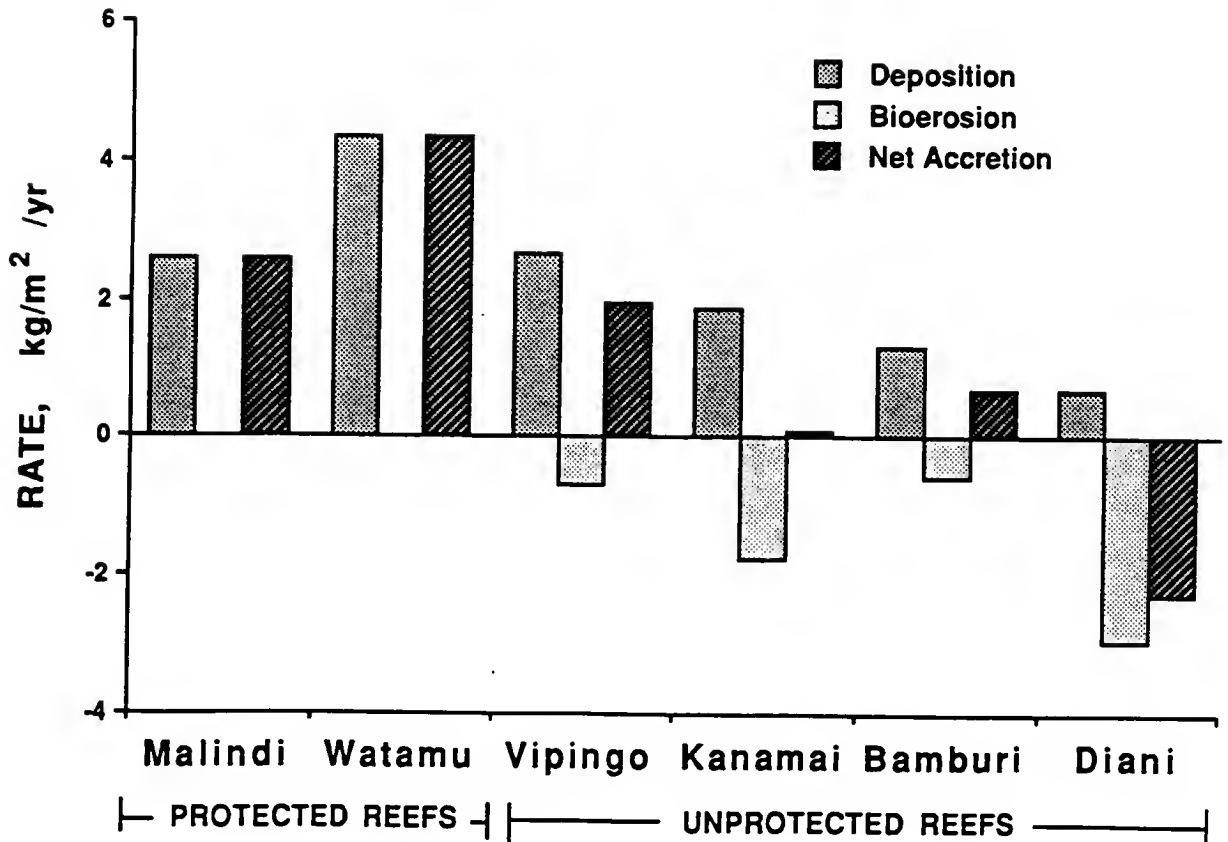
Fig. 39. Gross reef accretion, bioerosion and net growth of six Kenyan reef lagoons. Gross accretion determined by coral cover (Table 13) and calcium carbonate deposition equation (see Methods; Calcium Carbonate Deposition), and gross bioerosion by sea urchin densities (population density of urchins x bioerosion rate/urchin).
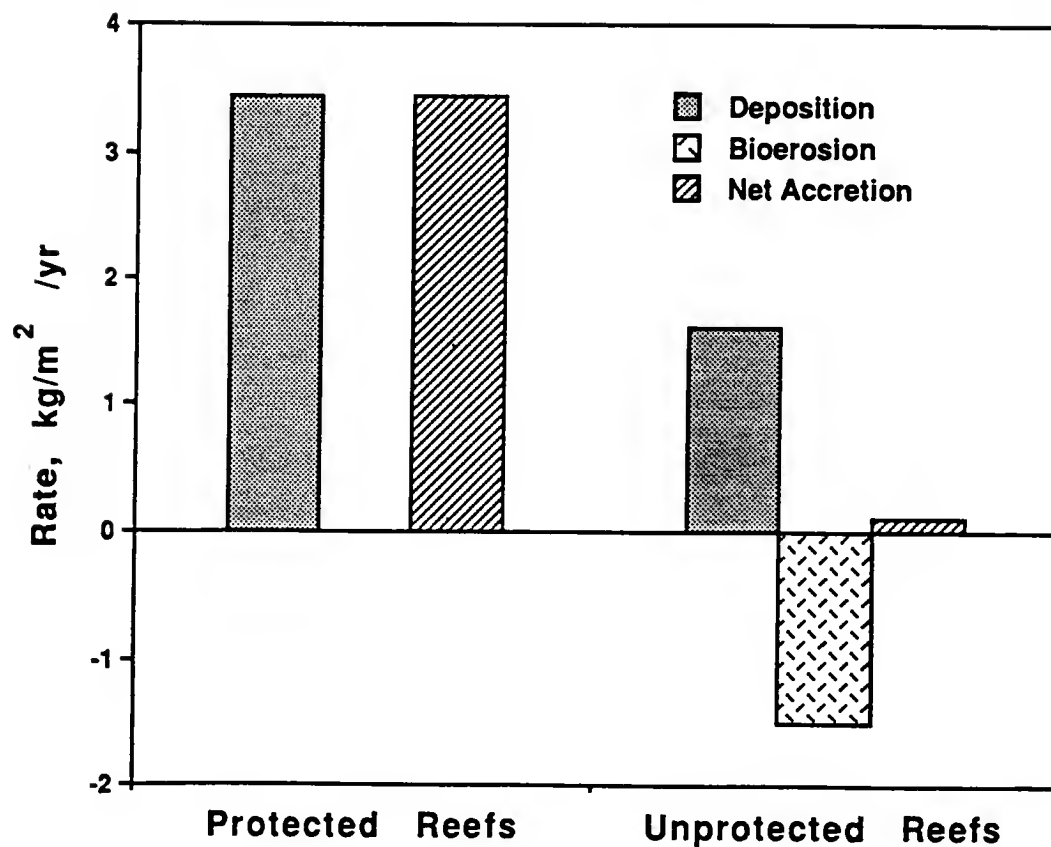
Fig. 40. The calcium carbonate balance of Kenyan reef lagoons based on the protected-unprotected classification. See figure 39 and methods section for details.

Model Results

Simulation of Competition and Predation with Minimodels

Minimodels with source-limited energy were developed to simulate the effects of different producer-consumer relationships. The model is presented in diagram form (Fig. 41), equations form (Table 21), and in the BASIC simulation program (Appendix A and B). The models differ from typical Lotka-Volterra models in having a source-limited flow in place of the usual constant "K" or population carrying capacity. An alternative model with a feedback from the consumer to the producer's production process was also evaluated (Fig. 42). The models were studied for the effect of (1) different rates of consumption, (2) different turnover rates of the organisms, and (3) different food limitations at steady state.

In order to study the effect of consumption and turnover rates on a consumer (F) the above model was first simplified to the environmental resource (RI), the primary producer (A), and the consumer (F). The consumer became the primary focus of the model manipulations. Studies on consumer energetics frequently report consumption rates of an organism as a percent of body weight, but in the calibration of coefficients the equations are such that the consumer's biomass cancels out of the equation and the steady state biomass is a function of the primary producer production rate and the consumer's consumption rate (for example see Table 23 equations for k5, k7 and k8). Consequently, the steady state biomass

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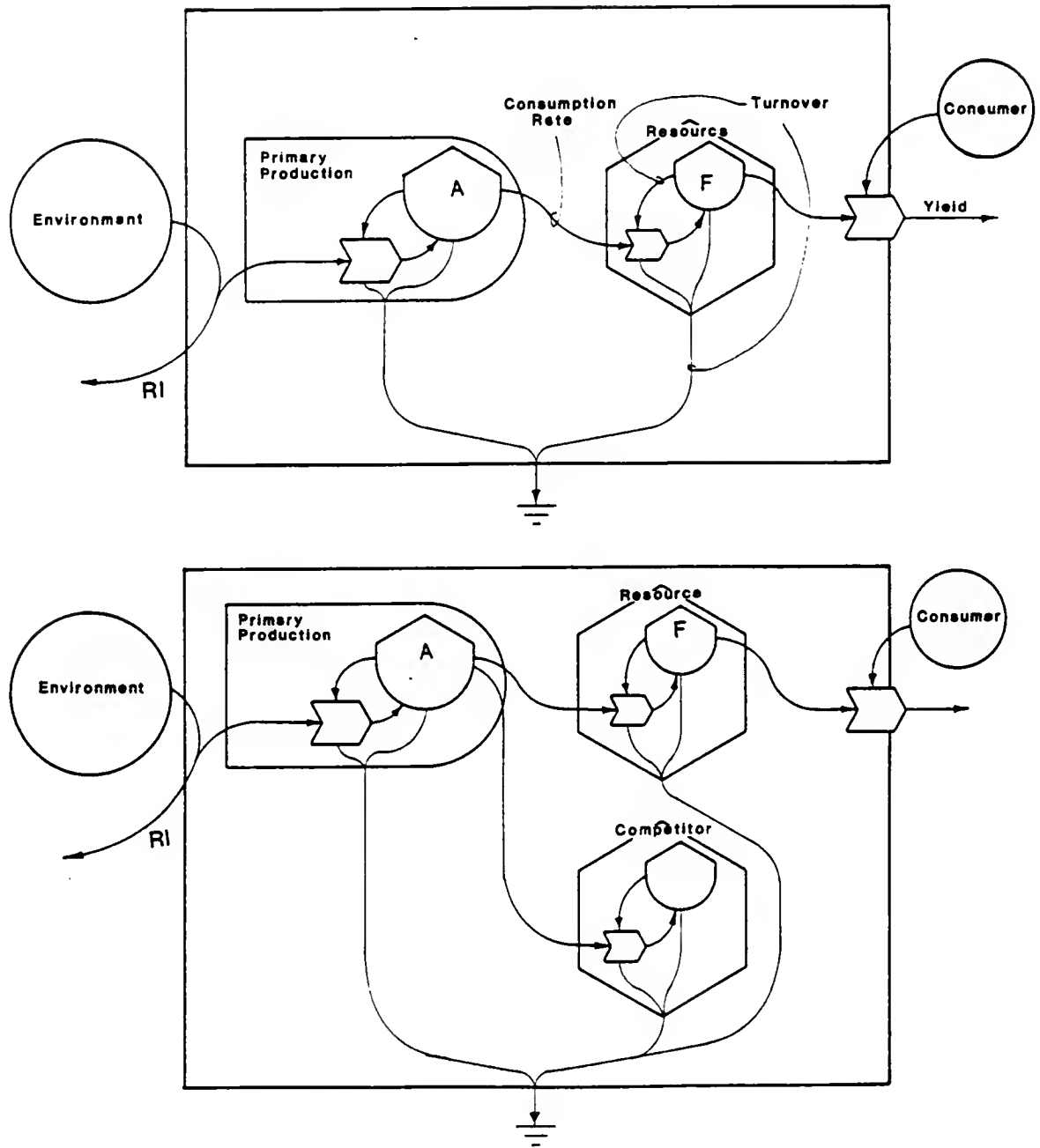
Fig. 41. Variations on the food chain model used to determine the role of turnover, feeding rates, and competition on yields to a consumer.

Table 21. Equations used in food chain models (Figure 41). Coefficient calculations given in Appendix B and C.

Equation	Variable
$RI = INS/(1+ k0\ A)$	Resource
$dA/dt = k\ A\ RI - k1\ A - k5\ A\ F$	Primary producer
$dF/dt = k7\ F\ A - k8\ F - k16\ M\ F$	Consumer 1 and 2
$dM/dt = k16\ M\ F$	Predator
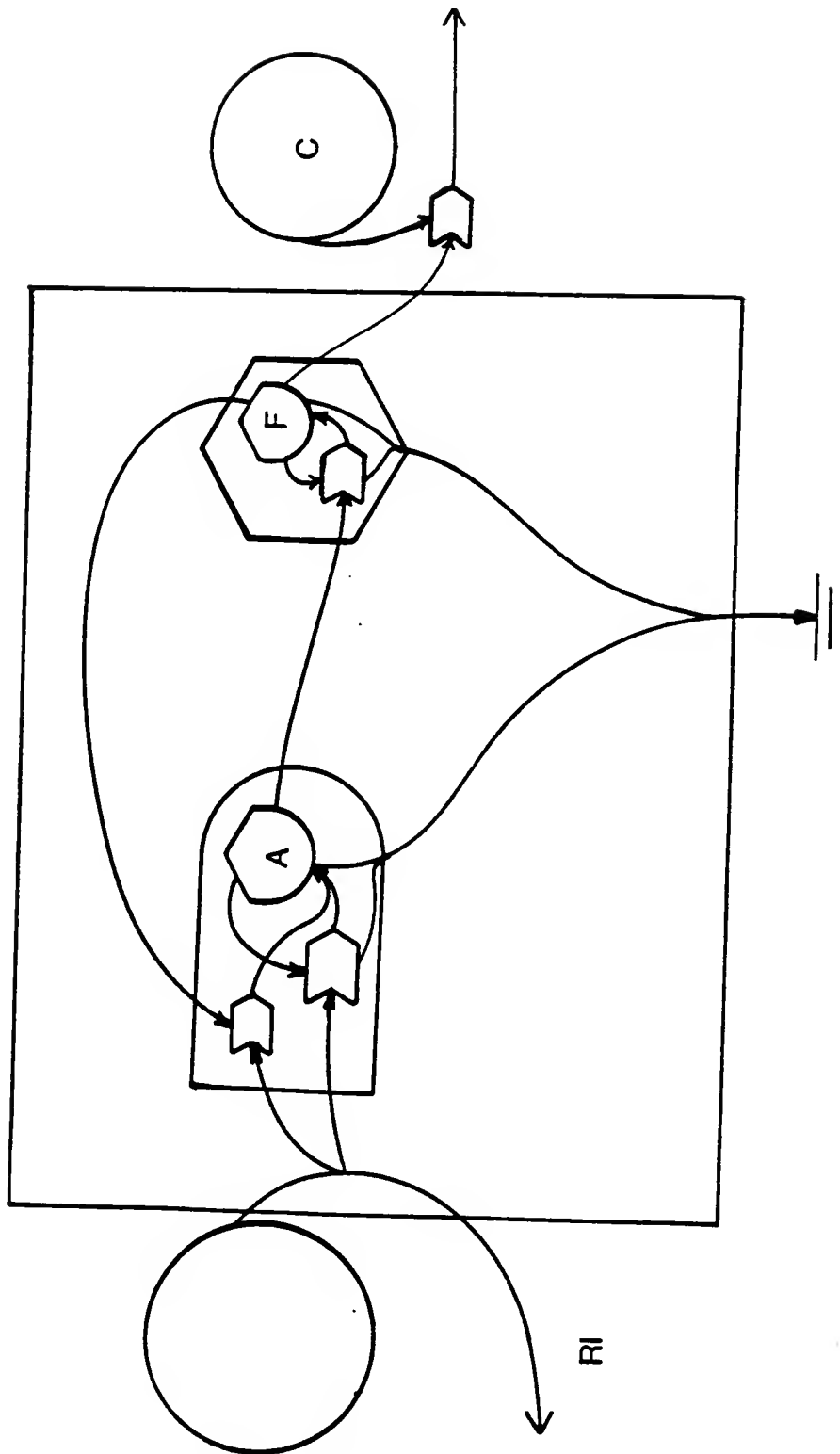
Fig. 42. Variation on the food chain model with feedbacks from the consumer to the producer.

of a trophic level can be determined for a given primary productivity and consumption rate.

Expected herbivore biomass plotted against reef production for different consumption rates (Fig. 43) indicates that steady state herbivore biomass increases with reef production and decreases with herbivore consumption when the consumer has no predators. Pandian and Vivekanadan (1985) report that consumption rates for tropical fish species range from 4 to 35% of their body weight per day with a mean of 16%. The expected biomass determined by this model is higher than reported for coral reef values (Goldman and Talbot 1976) because the model predicts biomass on for herbivores without the addition of higher trophic levels which would reduce the biomass of the herbivore.

To determine the effect of herbivore consumption and turnover rates on their contribution to the next higher trophic level the model was simulated for a variety of consumption and turnover coefficients (variations on Appendices B and C). Results indicate that herbivores with low consumption levels cannot tolerate high levels of predation (Fig. 44). The parabolic shape of the yield model suggests that the optimal yield to the consumer is a function of the herbivore's consumption rate. The higher the herbivores consumption rate the higher the tolerance of the herbivore to increased fishing. The absolute yield is always constant (i.e. 2000 kg/ha in the example given in Fig. 44) but the optimum is found at different consumer abundance values.

Changing the turnover rates of herbivores affects both the absolute yield and the level of consumption at which the optimal
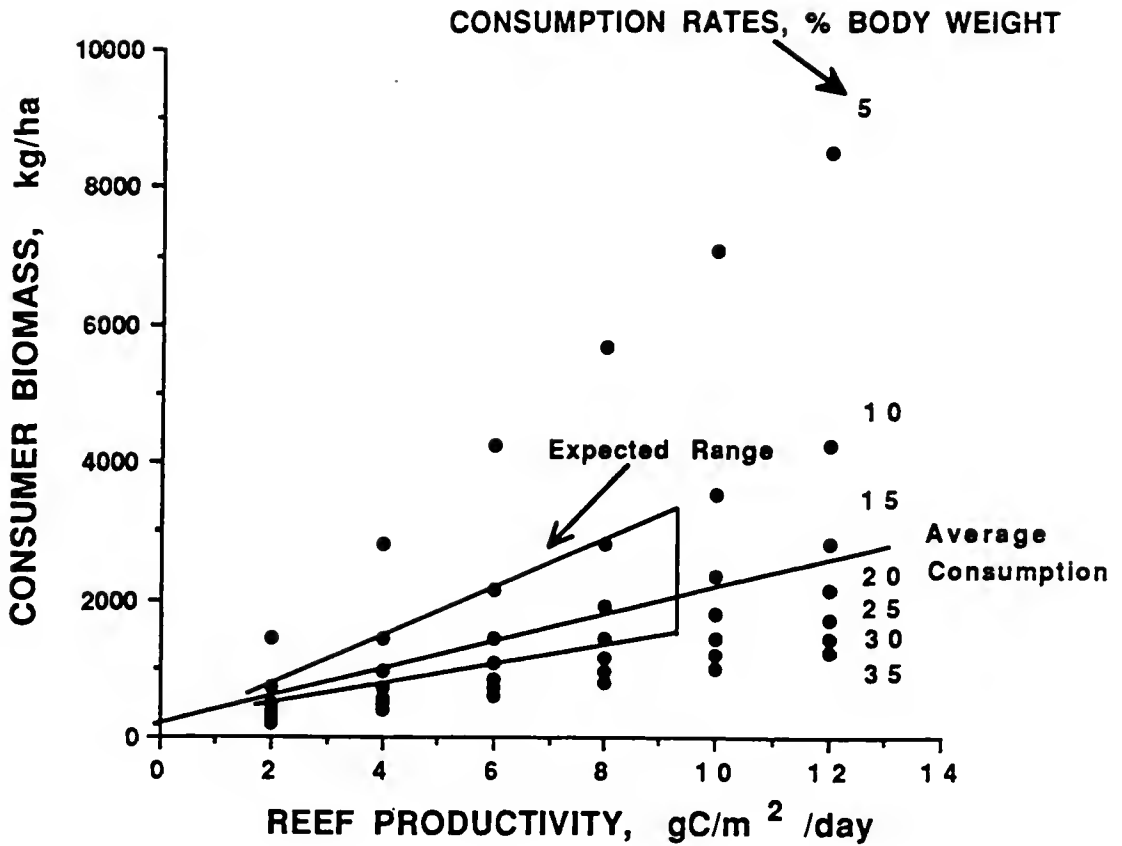
Fig. 43. Results of simulating the ·minimodel illustrated in
Figure 41 show the steady state values for the reef
productivity and herbivorous fish biomass in the absence of
predators for different fish consumption levels. Consumption is
expressed as a percent of the trophic levels biomass. Results
indicate the average and expected range based on a literature
review of Pandian and Vivekanandan (1985).
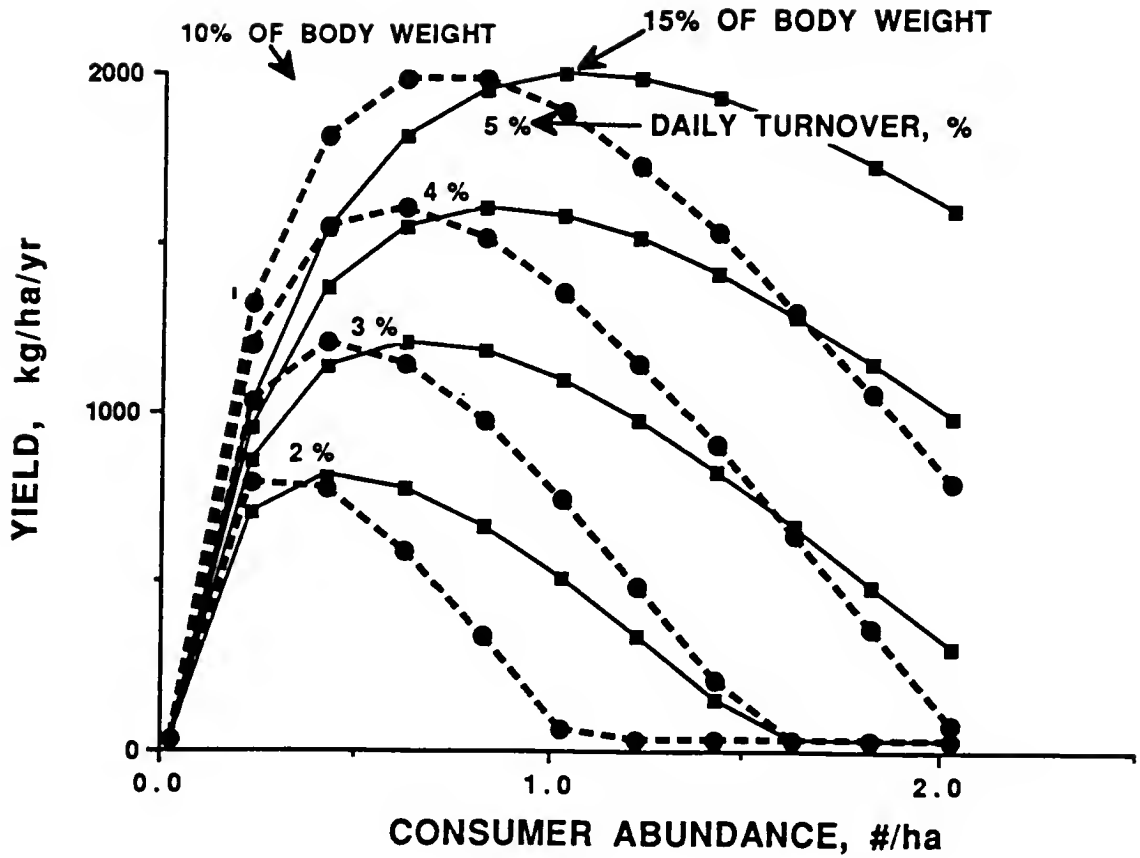
Fig. 44. Relationship between yield of prey to a predator (consumer abundance) for different prey consumption rates. Based on food chain model (Fig. 41). Simulation uses a consumer turnover rate of 5% per day and a reef gross production of 5 $gC/m^2/day$.

yield is obtained (Fig. 45). The lower the daily turnover, the lower the yield, and the lower the consumption of herbivores must be to obtain an optimum yield. This suggests that high yields can be expected for organisms with fast turnover times and that organisms with fast turnover can tolerate high rates of exploitation. Additionally, organisms with high consumption rates can tolerate greater rates of exploitation although their consumption rates will not affect the absolute quantity of the optimal yield

The level to which a consumer reduces its food resource will effect the consumers steady-state biomass (Fig. 46). Either under or "overgrazing" will result in a reduced biomass of the trophic level. In the example presented, maximum consumer biomass is achieved when consumers maintain their food resource between 20 and 30% of the food resources' maximum biomass.

The effects of a consumer feedback on production indicates that the addition of a feedback does not change the general shape of the producer and consumer charge up curves (Fig. 47a) but it can change their production and biomass. Simulations where the energy expenditure of a consumer was maintained constant (i.e. 5% of their energy consumption) while the effect on the producer was increased (Fig 47b) indicates that 1) the biomass of the producer is increased greatly and remains constant regardless of the rate of increase on production and 2) the consumer losses biomass by the feedback until the producer's production is increased substantially. In this example, by greater than 20%. Holding the increased production of the producer constant (i.e. a15% increase) and changing the energy expenditure of the consumer (Fig. 47c) suggests that 1) producer
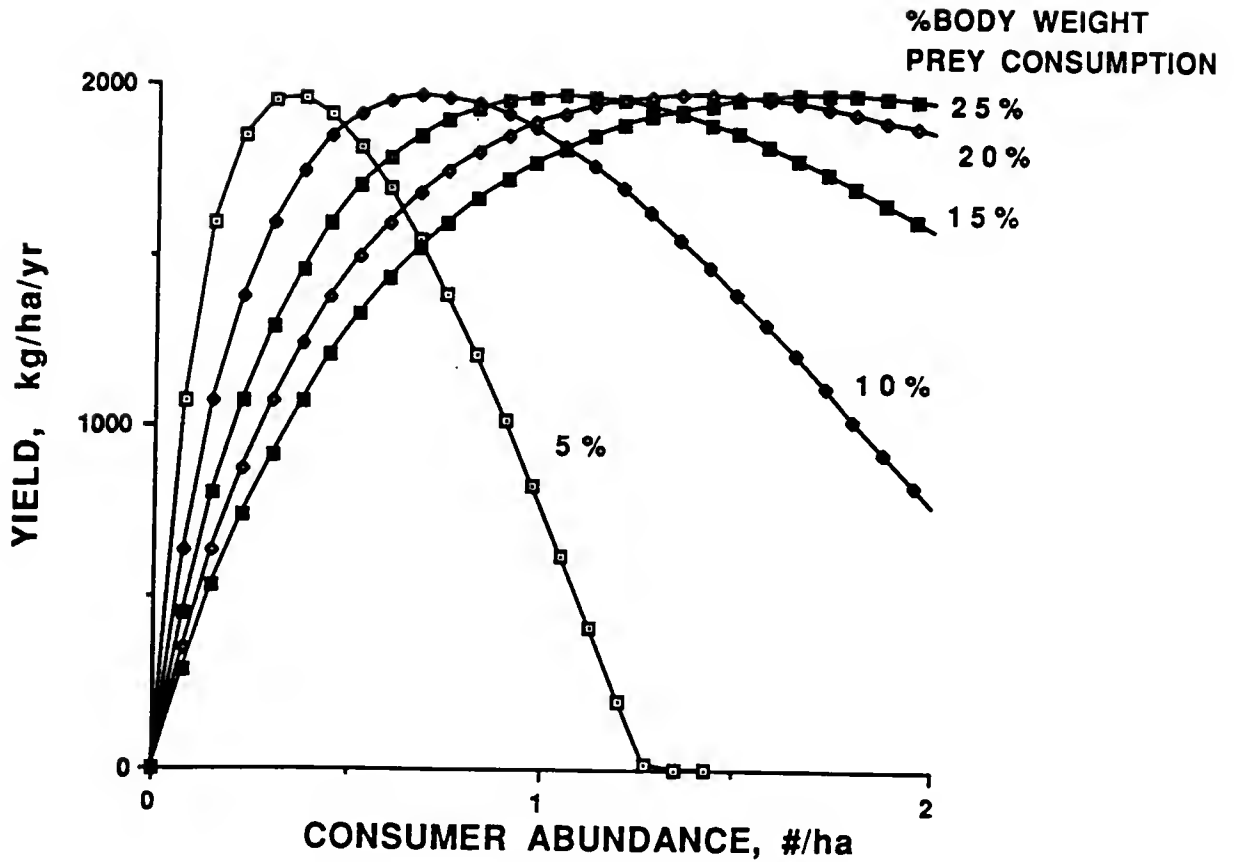
Fig. 45. Relationship between yield of prey to a predator for different prey turnover and prey consumption rates. Simulated for reef gross production of $5gC/m^2/day$.
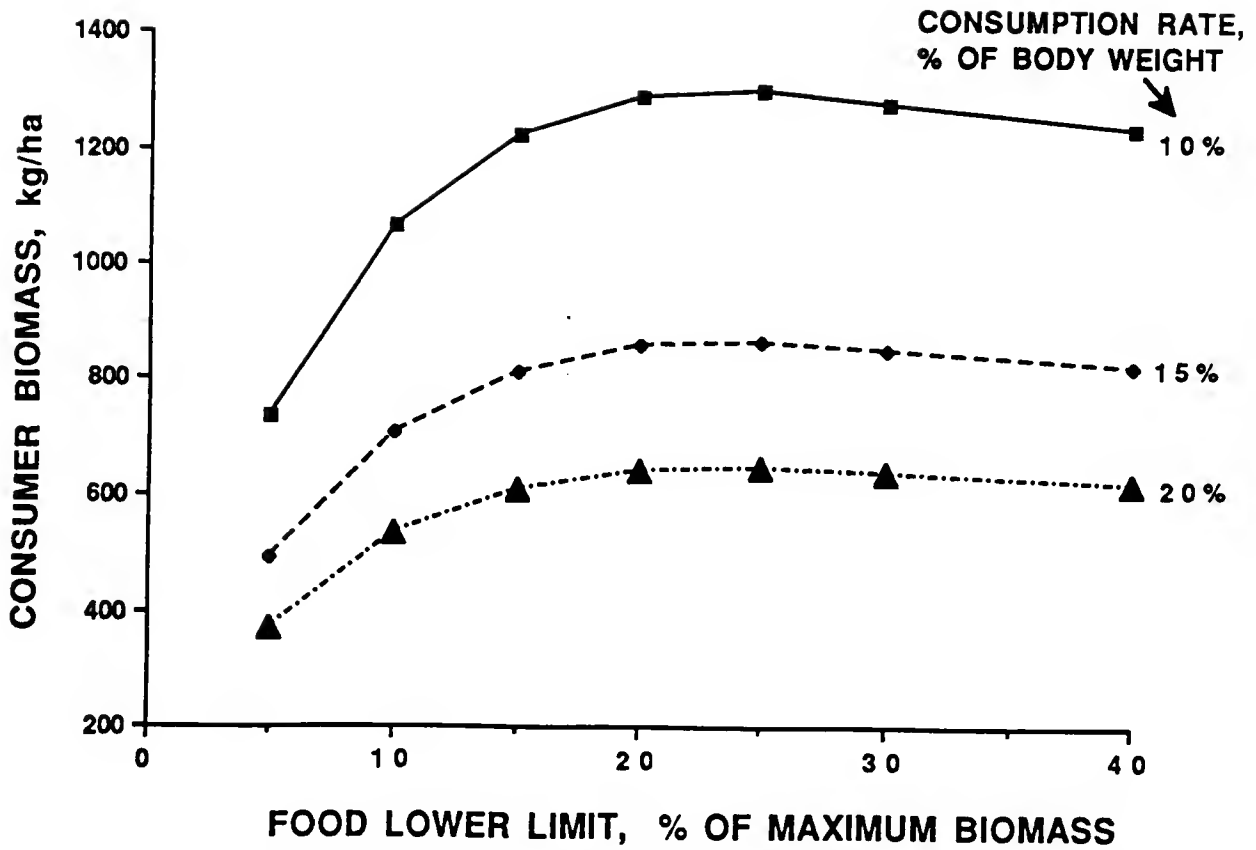
Fig. 46. Effect of the minimum food level on consumer biomass for different consumer consumption rates (% of body weight). Results are based on the food chain models illustrated in Figure 41. Gross production =5 $gC/m^2/day$.
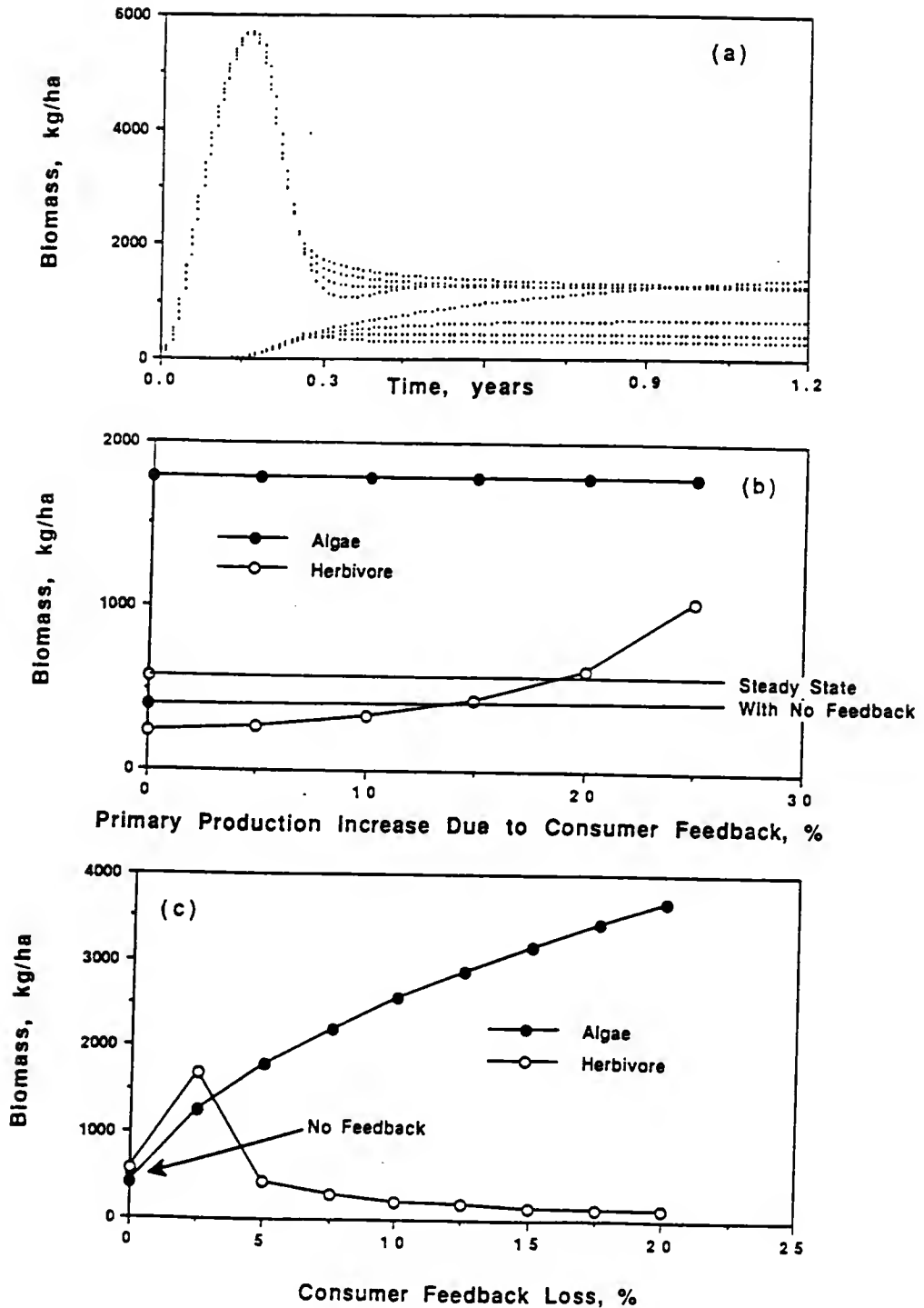
Fig. 47. Effect of consumer feedback on simple food chain model (Fig. 42). Charge up (a) of producer and consumer for different levels of consumer feedback (0 to 15% of consumption). Biomass (b) of producer and consumer for a constant consumer feedback (5% of its consumption) and an increasing effect on production. Biomass (c) of producer and consumer for a constant effect on primary production (15% increase) and an increasing consumer expenditure.

biomass rises asymptotically with consumer expenditure and 2) consumer biomass increases only at small energy expenditures (i.e. 2% of their energy consumption). Consequently, consumers may only develop feedbacks when energy expenditures are low (i.e. <5% of energy consumed) and the effect on production large (ie. >20% increase). This principle was used in feedback simulations added to the larger ecosystem model to follow.

Effects of consumption, turnover and minimum resource requirements on competitive ability and harvesting

Resource competition and interference competition are two general categories of competition. The classic Lotka-Volterra competition model utilizes a term (- kN_1N_2) in the inferior competitor's equation to account for competitive interactions. This term is representative of interference competition interactions as it implies a direct interaction between the two competitors. Less studied from a modelling approach is resource competition. Species utilizing the same resource can have variable consumption rates, turnover times and lower resource requirements. These factors are explored in the simple food chain model (Fig. 41) by the addition of a competitor that utilizes the same algal food resource.

If both competitors have precisely the same coefficients the biomass of each component is half of its value without a competitor such that the total biomass of the trophic level remains the same (Fig. 48). If consumption rates are changed then initial conditions are important (Fig. 49a). If both competitors are started with the
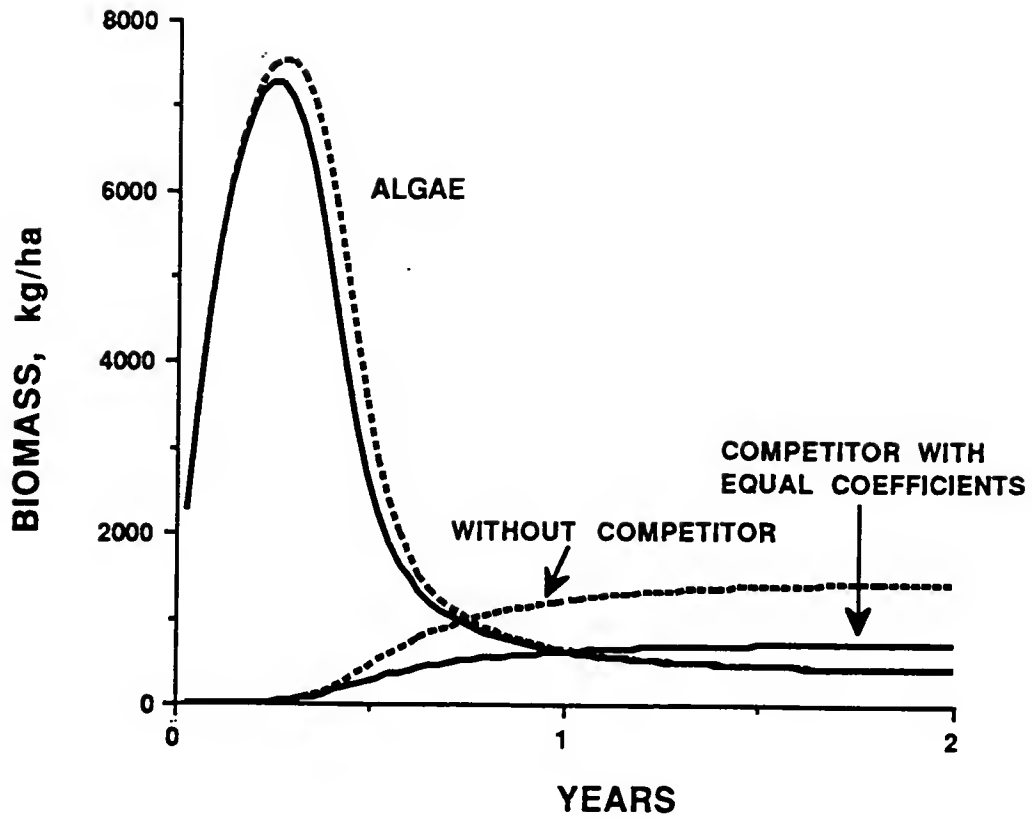
Fig. 48. Competition between two consumers with equal coefficients and for one consumer with the same coefficients.
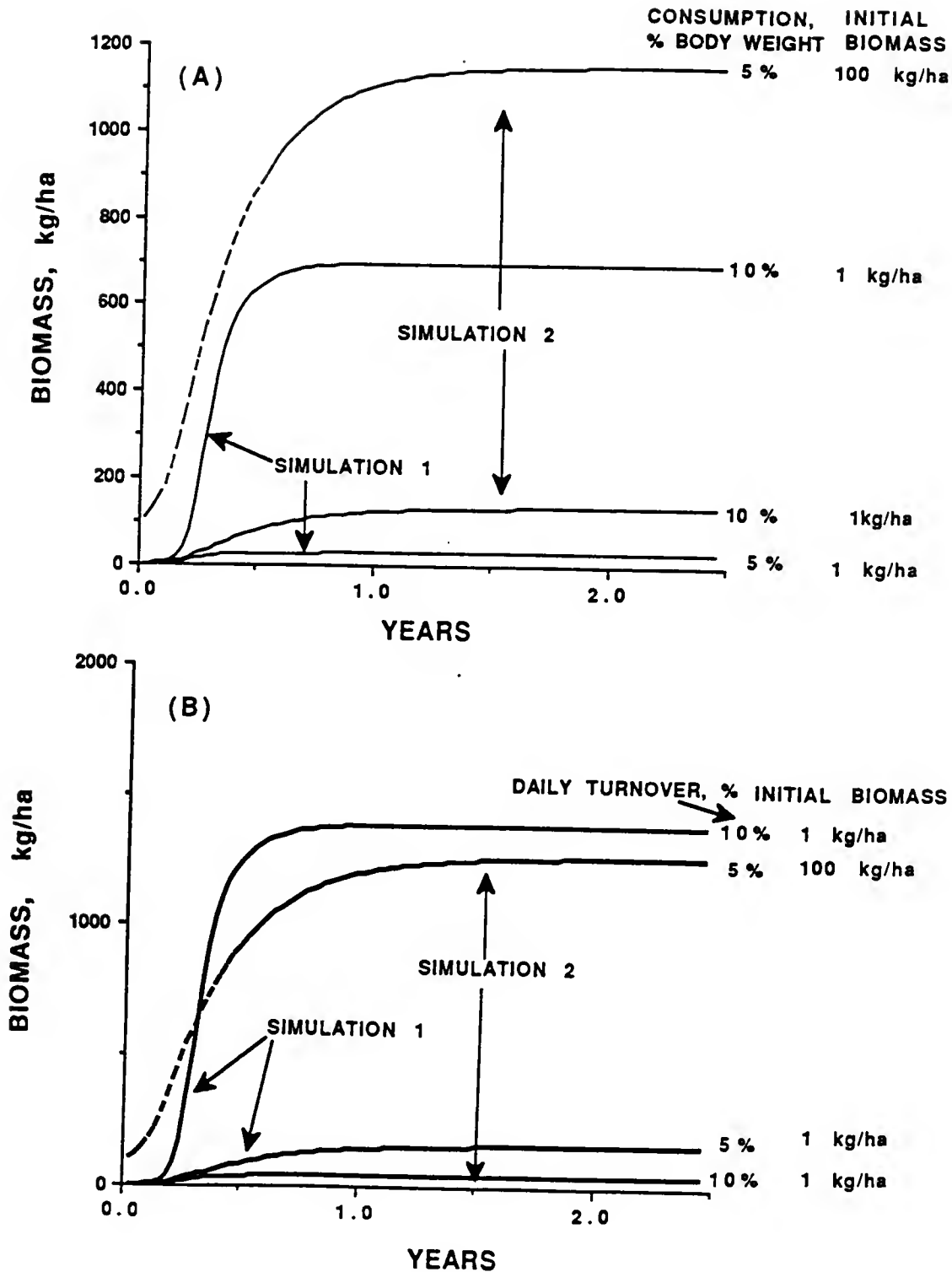
Fig. 49. (a) Competition between competitors with different consumption rates (% of body weight). (b) competition between competitors with different turnover rates (% turnover at maximum biomass). Includes two simulations with different initial conditions.

same initial biomass value, then the competitor with the higher consumption rate reaches a higher steady state biomass. But, if the competitor with the lower consumption rate is given an initially higher biomass value then it will achieve a higher biomass value than its competitor.

The result of changing turnover rates is also affected by initial conditions (Fig. 49b). If competitors are started at the same initial value, the competitor with the highest turnover rate reaches the higher steady state biomass. But, if the competitor with the lower turnover rate is given a higher initial value it will reach a higher biomass than its competitor. Regardless of the initial conditions, all competitors find a steady state and no competitor is "competitively excluded" such that their biomass approaches zero in these simulations.

When competitors are calibrated with lower resource limits the outcome of the competition is independent of initial conditions (Fig. 50). The species that has the lowest resource limit wins the competition regardless of initial conditions. If the lower food resource tolerance is maintained for one species and the competitor has a greater turnover or consumption rate (Fig. 51), the species with the lower food tolerance still wins the competition regardless of initial conditions. Consequently, the ability to tolerate lower resource abundance is more important for resource competition than are the turnover and consumption rates of competitors. From the yield models it is also clear that organisms with low turnover and consumption rates are less likely to tolerate intense predation and can only be superior competitors in the absence of predation.
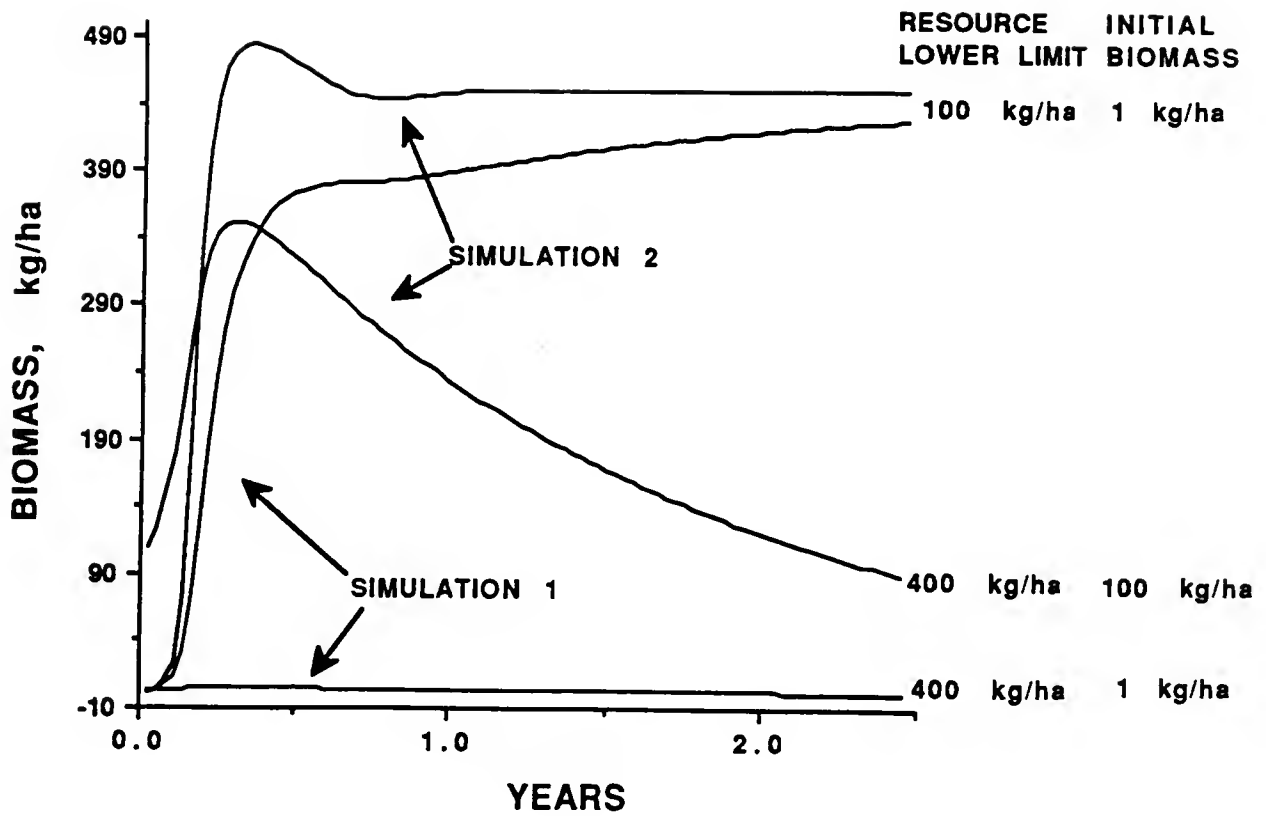
Fig. 50. Competition between competitors with different lower food resource limits. Includes two simulations with different initial conditions.
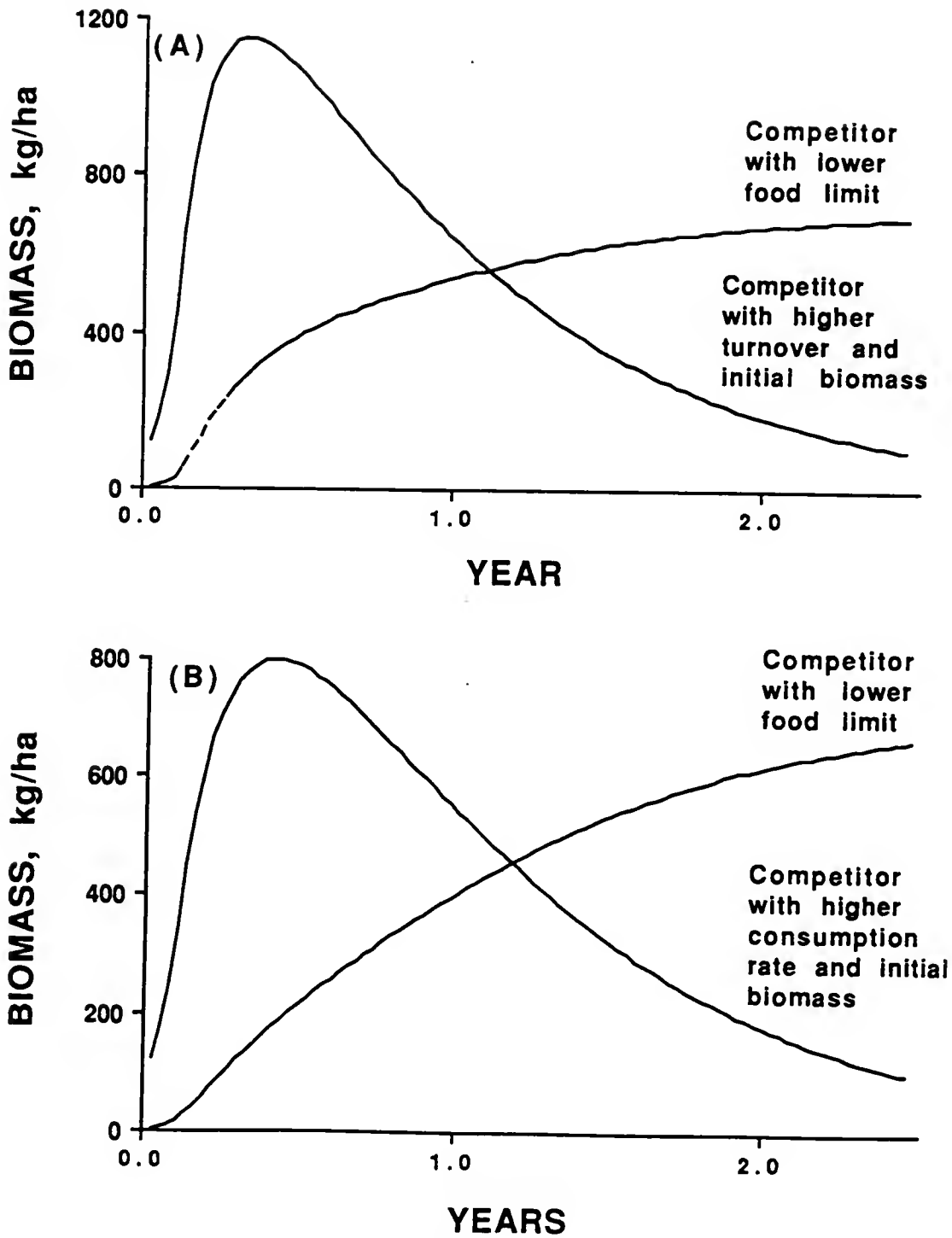
Fig. 51. Competition between competitors with different lower food resource limits and (a) different turnover times and (b) different consumption rates.

The addition of a higher level predator on eith one or both of the two competitors can have a dramatic effect on competitive ability (Fig. 52). If the consumer feeds on both competitors equally then competitive interactions remain unchanged. Yet, if consumption occurs only on the superior competitor (the species with the lower resource requirement) there is a critical consumption level at which the inferior competitor is able outcompete the superior competitor and drive its population to extinction. It is notable that in the simulation presented here this critical level occurs below the level of the optimal yield (i.e. Maximum Sustained Yield (MSY)) of the superior competitor. This suggests that MSY of multi-species fisheries may often be lower than the MSY calculated from single-species models particularly if competitors of the fisheries species are not harvested. Most real situations will have many species available which share similar resource requirements.

Coral Reef Ecosystem-Fisheries Model

A larger coral reef ecosystem-fisheries simulation model was developed using the main components of the coral reef that are believed to have major influences on grazing, the calcium carbonate balance and the control of these processes. A larger conceptual model was developed (Fig. 1) and from this a smaller simulation model was chosen for simulation (Fig. 53, Table 22).

The main features of the simulation model are two compensatory mortality interactions, one between algae and coral
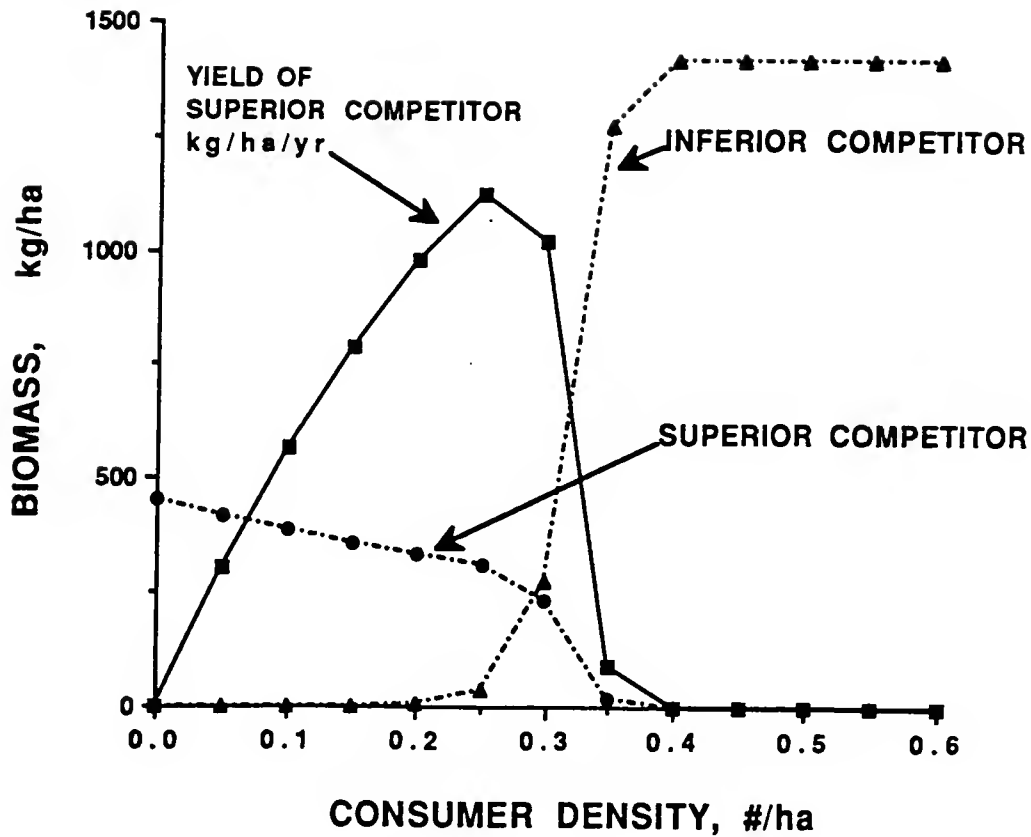
Fig. 52. Model of competition between two competitors where the superior competitor is preyed upon while the inferior competitor has no consumer. Plot of steady state biomass of the two competitors for different consumption levels of the superior competitor. Yield of the superior competitor is presented. Simulated with 5% turnover and consumption levels for each competitor and a primary production of 5g $C/m^2/day$.
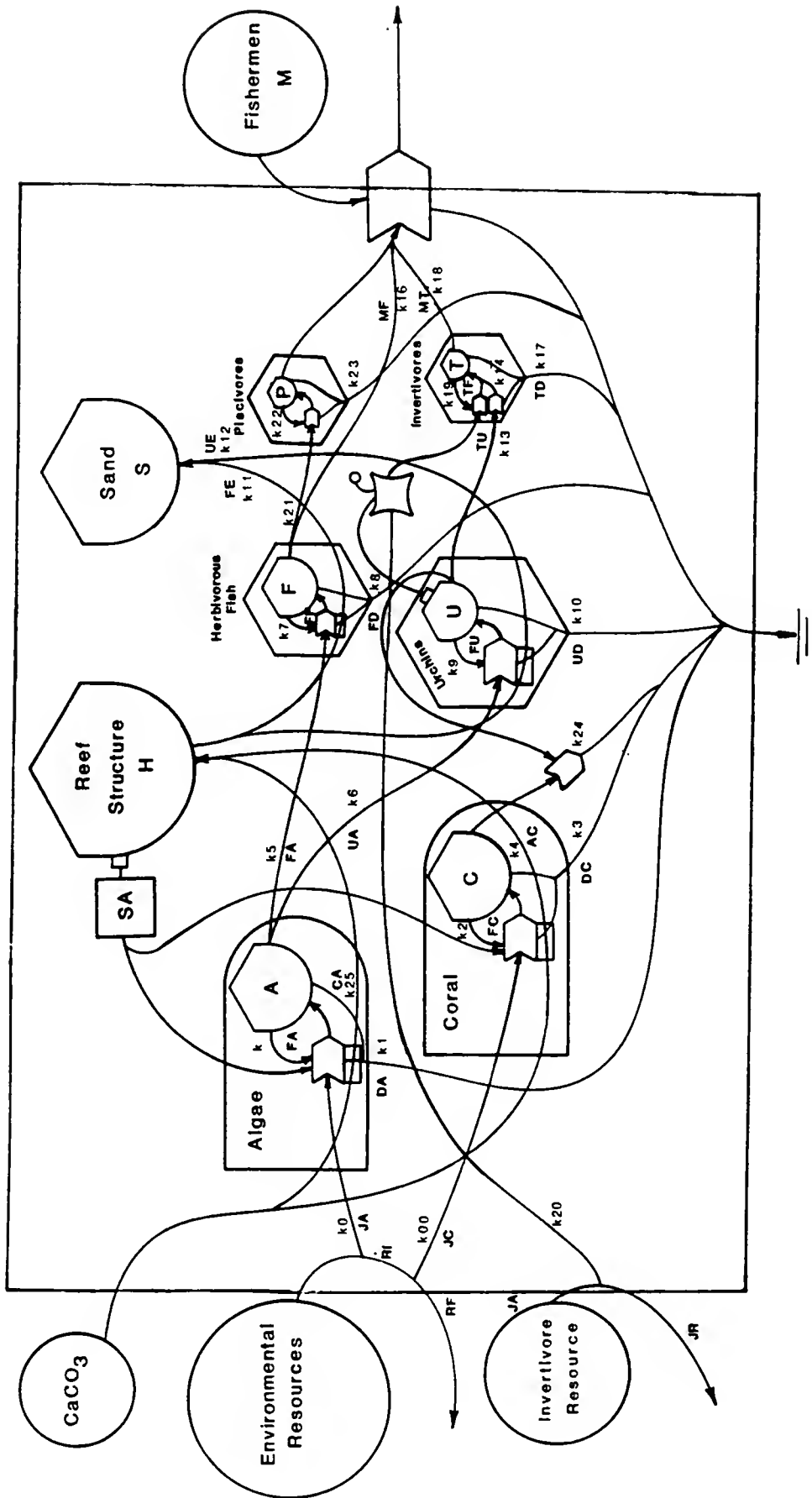
Fig. 53. Energy circuit diagram of the coral reef fisheries model.

Table 22. Equations used in the coral reef fisheries model (Figure 51).

Equation	Variable
Resource equations	
$RI = I/(1 + k0\ A\ SA)$	Resources used by algae
$RF = RI/(1 + k00\ C\ SA)$	Resources used by coral
$JR = RA/(1 + k20\ T\ (1-sw))$	Invertivore alternate resource
$sw = U^3/(100^3 + U^3)$	Switch for invertivores
Producer and Consumer equations	
$dA/dt = k\ A\ RI\ SA - k1\ A - k5\ A\ F - k6\ A\ U$	Algae
$dC/dt = k2\ C\ RF\ SA - k3\ C - k25\ C\ U$	Coral
$dF/dt = k7\ F\ A - k8\ F - k21\ P\ F - k16\ M\ F$	Herbivorous Fish
$dU/dt = k9\ U\ A - k10\ U - k13\ T\ U\ sw$	Sea Urchins
$dT/dt = T\ U\ k14\ sw + T\ JR\ k19\ (1-sw) - T\ k17 - MT\ T\ k18$	Invertivores
$dP/dt = k22\ P\ F - k23\ P - k18\ M\ P$	Piscivores
Substrate equations	
$SA = (3.60 + 6.72\ H)\ HHA$	Surface Area H=reef height, HHA=coral heads/ha
$dH/dt = k4\ C + k24\ A$	Calcium carbonate accretion
$dE/dt = k11\ F - k12\ U$	Bioerosion

and the other between herbivorous fish and sea urchins. Dominance of coral and herbivorous fish is maintained by predation on the competitive dominants (algae and sea urchins). Stability of the predators of invertebrates (invertivores) in the predator-prey interaction is maintained by the predator's ability to switch to an alternate food resource in the absence of sea urchins. Because invertivores (i.e. triggerfish) may feed on a variety of food resources in the absence of sea urchins (Reinthal *et al.* 1984), I added a general resource-limited food resource rather than attempting to account for multiple energetic pathways of this food resource.

The calcium carbonate balance is accounted for by coral deposition and sea urchin and herbivorous fish bioerosion. This model does not include other calcium carbonate deposition sources or physical forces of erosion. This is most likely to underestimate net erosion values. The addition of fishing allows model experimentation to determine the effect of different fishing levels on the model's components. Fishing experiments included: 1) fishing all fish components (piscivores, invertivores and herbivores) in proportion to their abundance, 2) fishing only piscivores, and 3) fishing only piscivores and herbivorous fish.

The coral reef fisheries model includes components of coral, algae, sea urchins, herbivorous fish, invertivores, piscivores, fishermen, reef structure and sand substrate (Fig. 51). Equations used in the simulation model are given in Table 22 and the calculated coefficients in Table 23. Simulating the model without herbivores indicates that algae are the superior competitors in the absence of herbivores (Fig. 54a, Appendix C). With the addition of

Table 23. Calculation of coral reef fisheries model coefficients. Equations use flows and storage symbols given in Figure 47. References refer to research where data was taken from or estimates based on.

Foot-note	Coefficient	Equation	References
1	$k0 = .00105$	$JA/(A*RI)$	Hughes et al (1987), Levitan (1988)
2	$k00=0.00128$	$JC/(C*RF)$	Lewis (1981)
3	$k=0.0000134$	$FA/(A*RI)$	Lewis (1977)
4	$k1=0.0588$	DA/A	" " "
5	$k2=0.000024$	$FC/(C*RF)$	" " "
6	$k3=0.1042$	DC/C	" "
7	$k4=0.023$	AC/C	Smith (1983)
8	$k5=0.000157$	$FA/(F*A*0.16)$	Goldman & Talbot (1976), Hatcher (1981)
9	$k6=0.000167$	$UA/(U*A*0.035)$	Muthiga & McClanahan (1987), Hawkins & Lewis (1982), Levitan (1988,1989), Foster (1987), Carpenter (1981), Hughes et al. (1987)
10	$k7=0.0000102$	$FF/(F*A*0.22)$	Hatcher (1981)
11	$k8=0.0022$	FD/F	" "
12	$k9=0.0000016$	$FU/(U*A*0.035)$	Hawkins & Lewis (1982)
13	$k10=0.005$	UD/U	" "
14	$k11=0.00904$	FE/F	Birkeland (1988)
15	$k12=0.0168$	UE/U	This study and Birkeland (1988)
16	$k13=0.0008$	$TU/(T*U*0.01)$	McClanahan & Muthiga (1989)
17	$k14=0.000008$	$TF/(T*U*0.01)$	Estimated
18	$K16=0.04$	MF/F	Estimated
19	$K17=0.0004$	TD/T	Estimated
20	$k18=0.04$	MT/T	Estimated
21	$k19=0.00008$	$TF/(T*JR)$	Estimated
21	$k20=0.128571429$	$(JA-JR)/(T*JR)$	Estimated

Table 23-cont'd

Foot-note	Coefficient	Equation	References
22	k21=0.00008	FP/(F*P)	Estimated
23	k22=0.0000008	FP*.01/(F*P)	Estimated
24	k23=0.0004	FP*.01/P	Estimated

1) The resource here is assummed to be sunlight with incoming intensity of 43,835 Joules/ha/day, 10% of this is unavailable at maximum algal biomass. Maximum algal dry weight from Hughes et al. (1987).

RI=43,835*0.1 Joules/ha/day
A=8500 kgdw/ha
JA=43,835*0.9 Joules/ha/day

2) Same assumption as above but maximum coral biomass used calculated at 100% cover at 0.048 g/cm2 (wet) estimated from Lewis (1981).

RF=43835*0.1
C=4800 kg/ha
JC=43835*0.9

3) Assumes GPP of 10 gC/m2/day (Lewis 1977) which is 500 g/ha/day (wet) if one assume 50 % carbon and 40% dry to wet weight ratios.

FA=500 gdw/ha/day

4) Algal depreciation assumed equal to production at high biomass values

FD=500 gdw/ha/day

5) See footnote 3.

6) Assume depreciation equals production at maximum biomass

DC= 500 gdw/ha/day

7) Assumes that at maximum coral cover CaCO3 production equals 4 kg/m2/year (Smith 1983)

AC=110 kg/ha/day

8) Maximum herbivorous fish biomass assumed 35% of total maximum fish biomass (this study) which Goldman & Talbot (1976) estimate at 2000 kg/ha. Algal biomass is 16% of maximum or 1400 kg/ha (Hatcher 1981). Herbivorous fish remove ca. 22% of their biomass per day (Hatcher 1981).

Table 23-cont'd

F=700 kg/ha (wet)
FA=154 kg/ha/day

9) Maximum urchin biomass assumed to be ca. 500 g/m2 (Muthiga & McClanahan (1987), Levitan (1988,1989). Algal biomass is 3.5% of maximum biomass at maximum sea urchin densities (Hughes et al. 1987, Carpenter 1981, Carpenter 1988, Levitan 1988).Sea urchins remove ca. 5% of their biomass per day (Hawkins & Lewis 1982, Carpenter 1988, this study).

U=5000 kg/ha (wet)
UA=250 kg/ha/day

10) Herbivorous fish eat 22% of their biomass per day (Hatcher 1981) and assuming a 1% biomass turnover per day.

FF=1.54 kg/ha/day

11) Assumes that total gross production consumed by population at maximum biomass

FD=1.54 kg/ha/day

12) Sea urchins eat ca. 5% of their biomass per day (see reference in footnote 9) and assume a 1% daily biomass turnover.

FU= 2.5 kg/ha/day

13) Assumes gross production equals consumption at maximum biomass

UD=2.5

14) Bioerosion by herbivorous fish equal to 0.452 g/day at maximum biomass Birkeland (1988).

FE=4.52 kg/ha/day

15) Urchin bioerosion .42 g/urchin/day at maximum urchin biomass which equals ca. 8.4 g/m2/day.

UE= 84 kg/ha/day

16) Triggerfish are found at ca. 70 kg/ha in protected reefs (this study) and urchins 1% of their maximum biomass when invertebrate predators most abundant. Triggerfish eat 4% of their biomass per day

T=70 kg/ha
TU= 2.8 kg/ha/day

17) Assumes a biomass turnover of 1% per day.

TF=0.028 kg/ha/day

18) Assumes a man can catch 20 kg/ha/day of herbivorous fish at maximum fish biomass

Table 23-cont'd

MF=20 kg/ha/day

19) At maximum biomass losses equal gains

TD=0.0.028 kg/ha/day

20) Assumes a man can catch 2.8 kg/ha/day of invertebrate predators at maximum fish biomass

MT= 2.8 kg/ha/day

21)These values assume that triggerfish are able to find another food resource in the absence of sea urchin and will maintain the same production as above.

JA= 49.3   49.3
JR = 4.93   4.93

22) Assumed piscivorous biomass equals 25 kg/ha and that they consume 4% of their body weight per day.

P=25 kg/ha
FP = 1

23) Assumes biomass turnover of 1% per day

24) Assumes depreciation equals production at maximum biomass
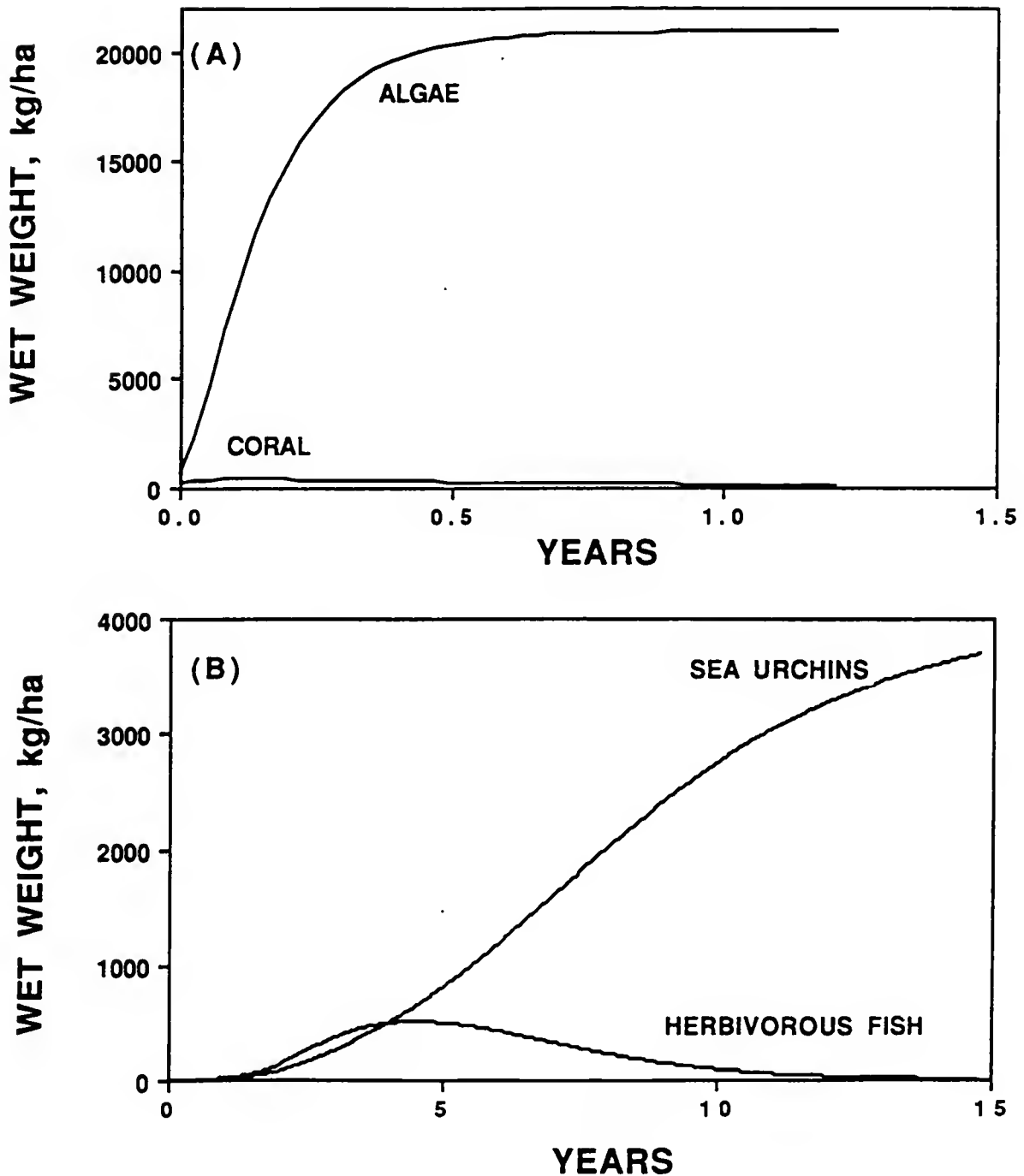
Fig. 54. Result of simulaing the coral reef fisheries ecosystem model (Figure 53) for two simulations (a) coral and algal relationship in the absence of herbivory on algae and (b) algae, coral, sea urchin, herbivorous fish relationship in the absence of piscivores and invertivores.

herbivores and the absence of carnivores, coral reaches a higher biomass than without herbivores, and sea urchins are superior competitors than herbivorous fish (Fig. 54b, Appendix D). With the addition of carnivores, herbivorous fish maintain a higher biomass than sea urchins (Fig 55).

In order to determine the role of fishing on reef processes and components, the model was simulated for various fishing levels (Appendix E). Fishing intensity was adjusted and the model allowed to run (30 years) until a steady state was reached. Based on this model, reef structure never reaches a steady state and either continues to increase or decrease indefinitely. Reef structure was started at about 1.5 E+6 kg/ha and final values should be compared to this initial value to determine if a decrease or increase has occurred during the 30 years. Values at 30 years were plotted against fishing level.

The first fishing experiment removed some of all fish components (piscivores, invertivores and herbivores). Results indicate that the biomass of fish is reduced, sea urchin populations increase, and accretion of the calcium carbonate becomes negative with increasing fishing intensity (Fig. 55). The simulation also indicates that there is a rapid transition between fish and sea urchin dominated ecosystems at about 0.05 fishermen per hectare or 350 kg/ha/yr. Maximum fish yield (about 380 kg/ha/yr) is obtained at 0.05 fishermen/ha which is short of the projected MSY without sea urchins as competitors for algae. Fish yield drops dramatically after the critical transition occurs and is reduced to zero after sea urchins dominate the algal resource. Reef growth and calcium carbonate

Fig. 55. Coral reef ecosystem fisheries model for different levels of the fishing when all three fish components (piscivores, herbivores and invertivores) are fished. Plotted values are values after 30 years of simulation at different fishing intensities (fishermen/ha).
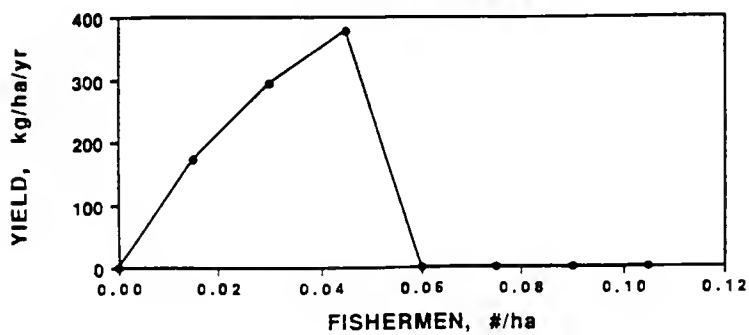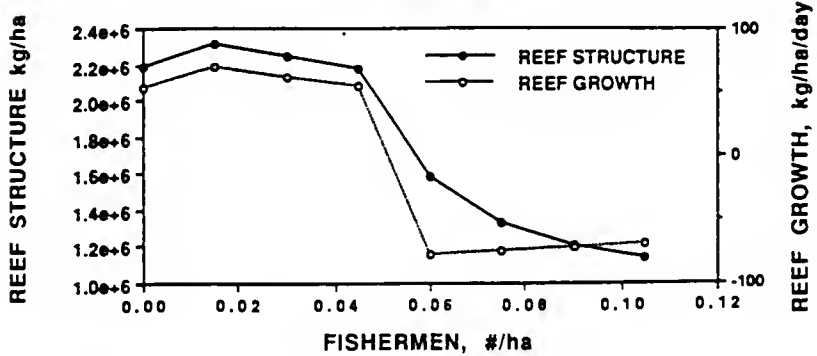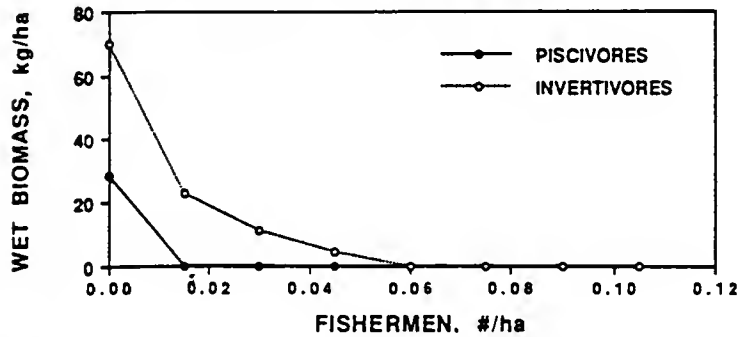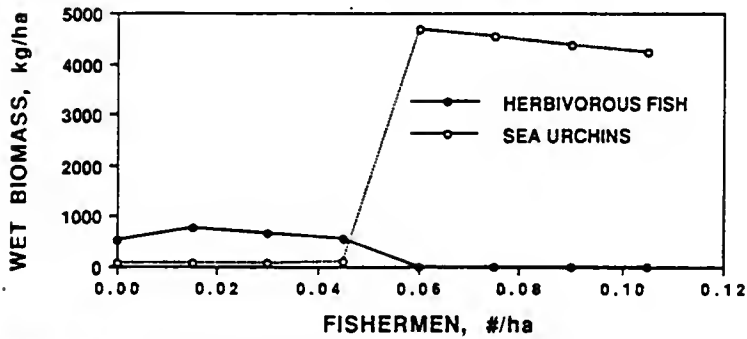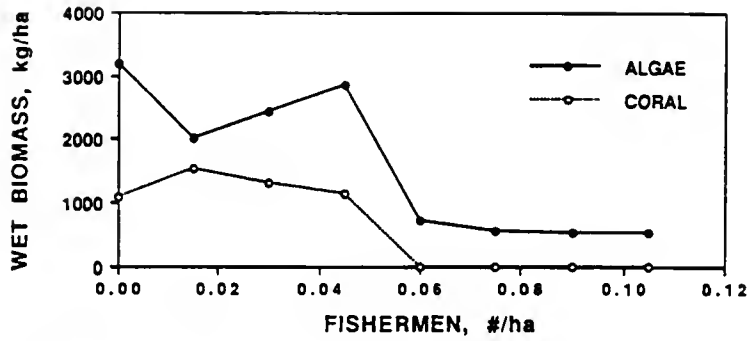
accretion decrease with fishing intensity. The decrease is most rapid when sea urchins become the dominant grazers. Reef structure decays as the accretion rate becomes negative.

Fishing only the piscivores (Fig. 56) results in higher herbivorous fish and coral abundance and a resultant increase in reef accretion and growth rates. Yet, fish yield is very low (<1 kg/ha/yr) and maximum yield is obtained at a fishing intensity an order of magnitude below the above model (0.004 fishermen/ha). Invertivores and sea urchins are maintained at their initial values.

Fishing piscivores and herbivorous fish (Fig. 57) produces the greatest fish yield 600 kg/ha/yr and at the highest fishing intensity (0.16 fishermen/ha). Piscivores are quickly reduced and this releases the herbivorous fish from their natural mortality. The herbivores are able to reach a higher biomass, in the absence of predators, and at this point they supply all of the fisheries yield at the MSY. Algal biomass increases and coral decreases with increasing fishing intensity. Nevertheless, reef accretion rates and growth remain positive although reduced somewhat from pristine conditions.

Two simulations were completed with the ecosystem model adding feedbacks. The first simulation added feedbacks from herbivorous fish to coral and algal components (Fig. 58) while the second added feedbacks from both herbivorous fish and sea urchins to coral and algae (Fig. 59). Both simulations suggest that feedbacks 1) increase fisheries yields at low levels of fishing but 2) models with feedbacks are perturbed and switch to a sea urchin-dominated reef at lower fishing intensity. In both simulations algal biomass is
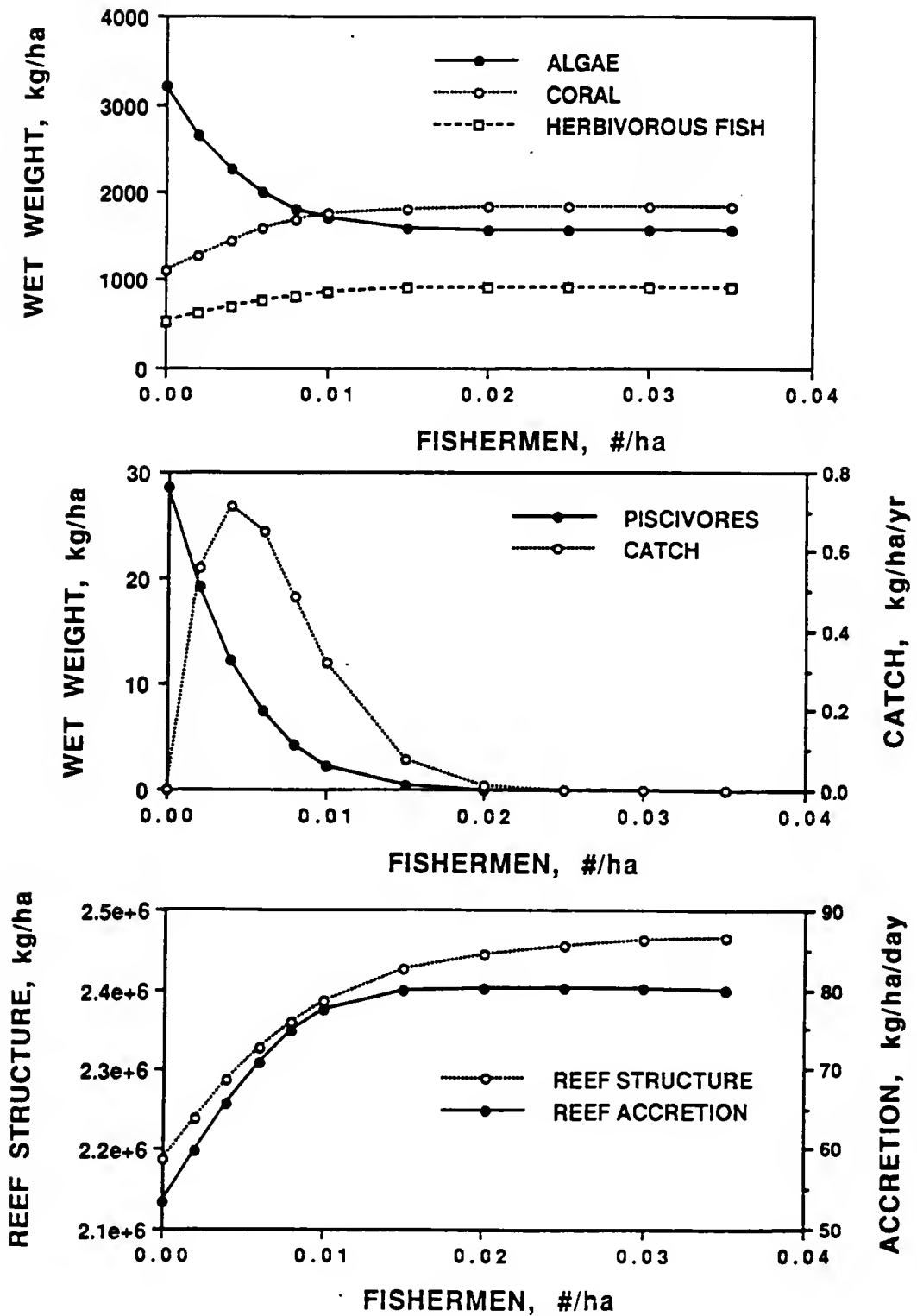
Fig. 56. Coral reef ecosystem model output (after 30 years of simulation) when only piscivores are fished. Invertivore and sea urchin populations remained near their initial conditions are, therefore, not plotted.

Fig. 57. Coral reef ecosystem model output (after 30 years of simulation) when only piscivores and herbivorous fish are fished. Invertivore and sea urchin populations remained near their initial conditions are, therefore, not plotted.
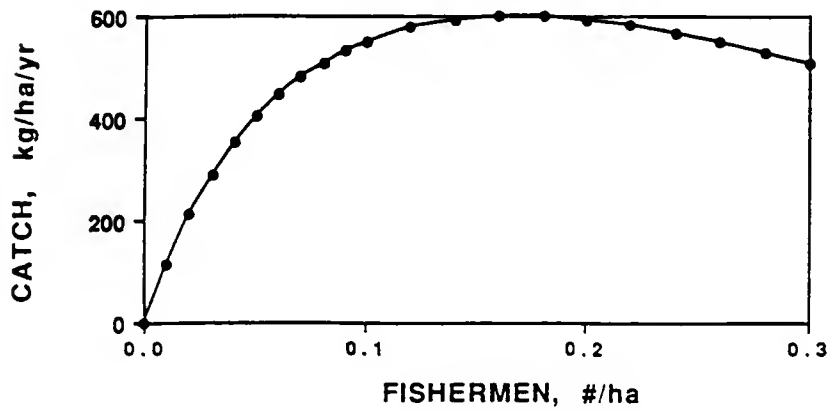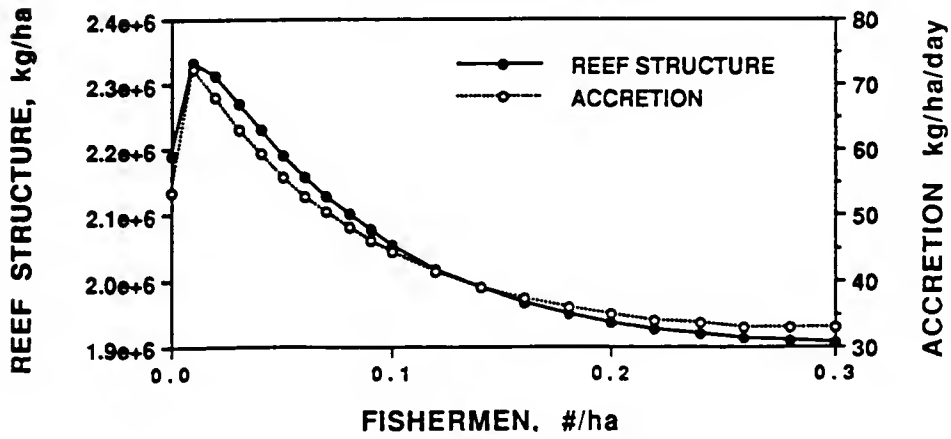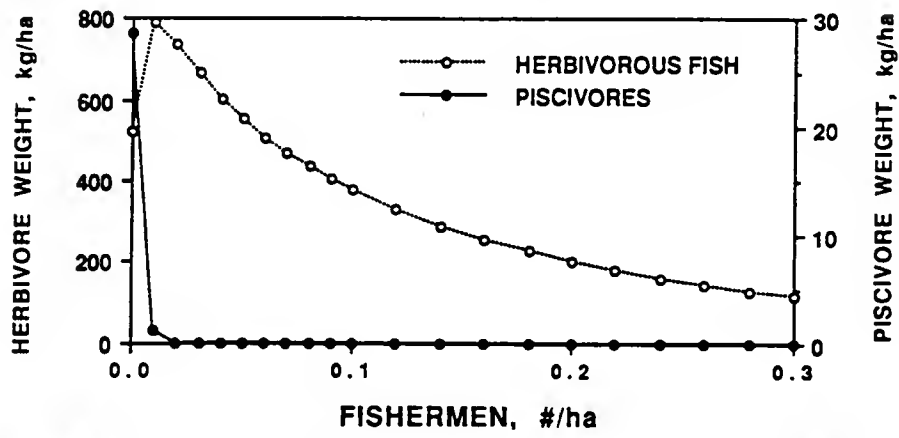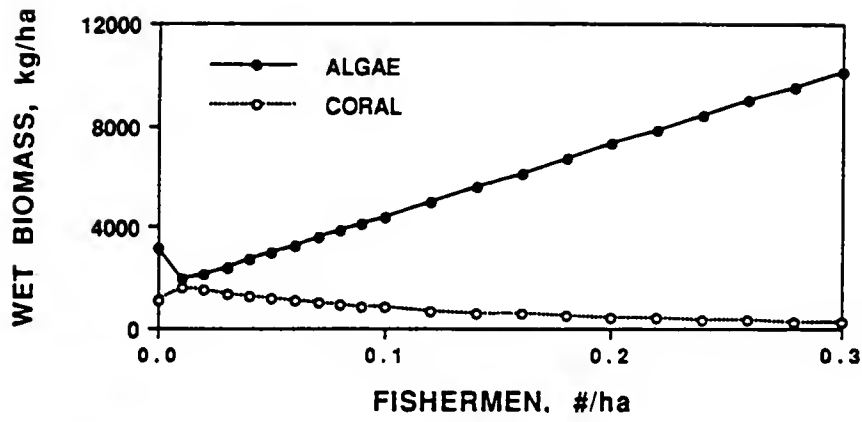
Fig 58. Coral reef ecosystem model output when feedbacks from herbivorous fish to coral and algae is added. Herbivorous fish expends 2.5% of its energy gained in consumption which increases primary production of each component by 20%.

Feedback to Producers from Urchins and Herbivorous Fish
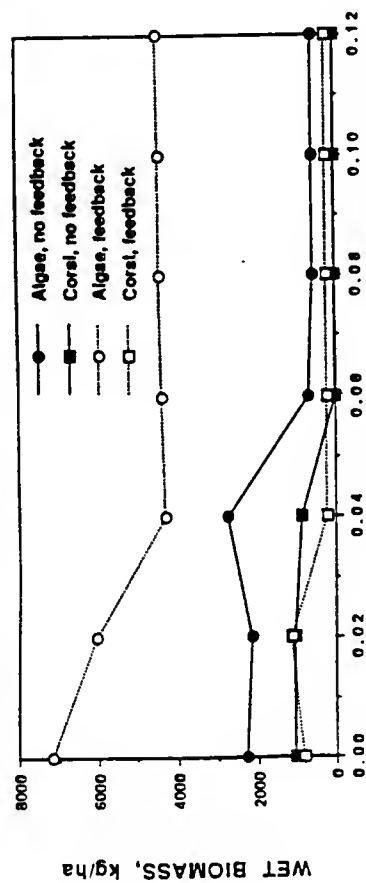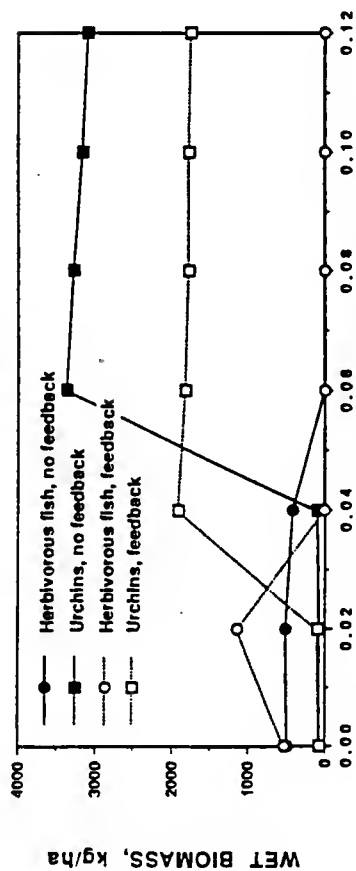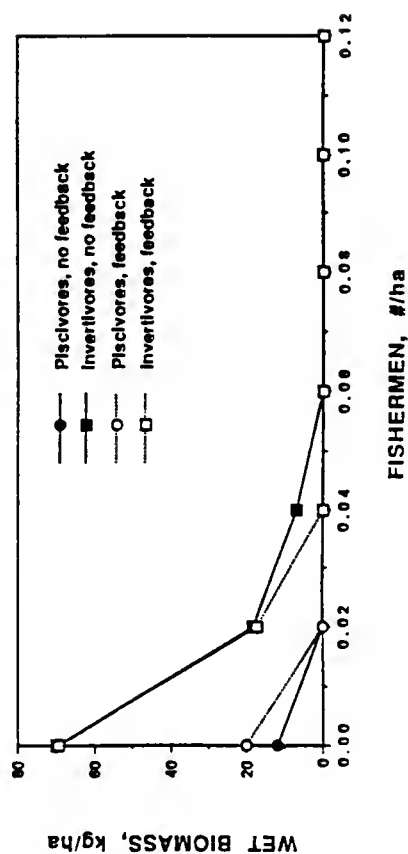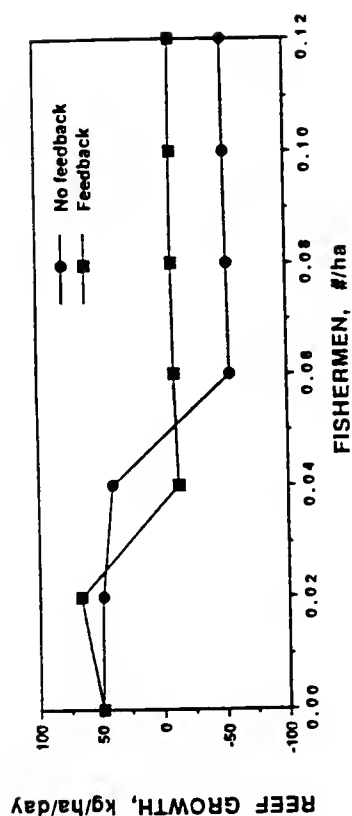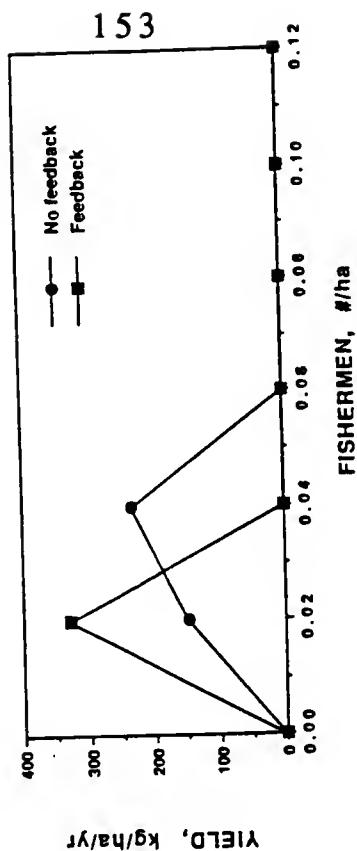
Fig. 59. Coral reef ecosystem model output when feedbacks are added from both herbivorous fish and sea urchins. Both herbivores expend 2.5% of it energy consumption and increase primary production components by 20%.

Feedback from Herbivorous Fish to Coral and Algae
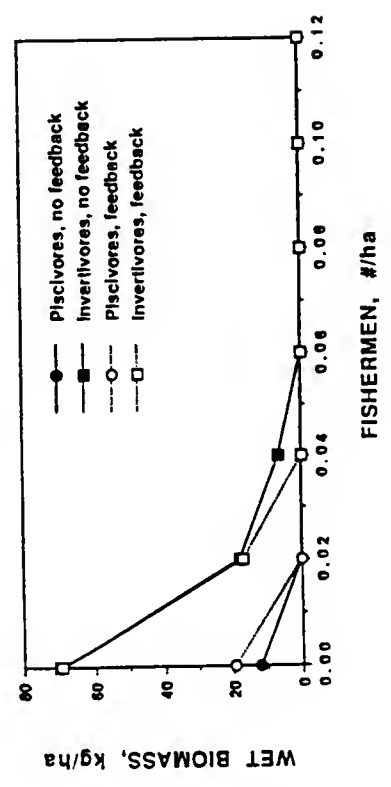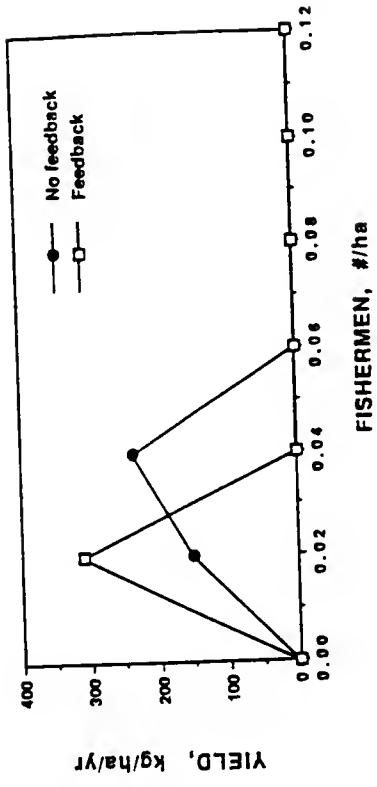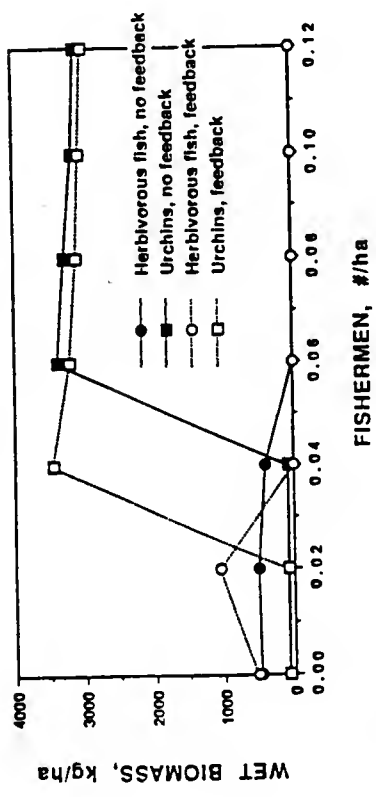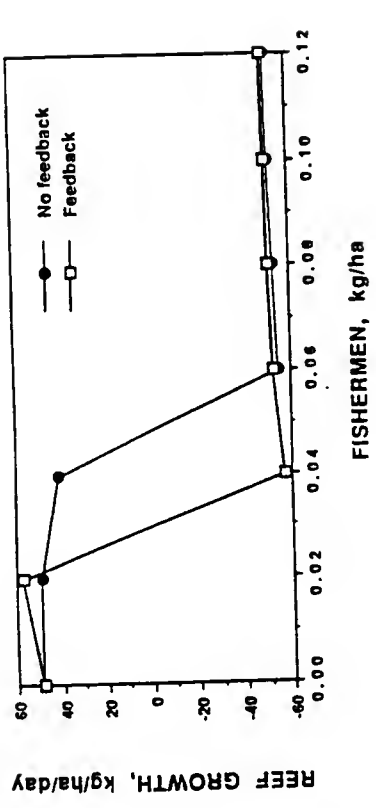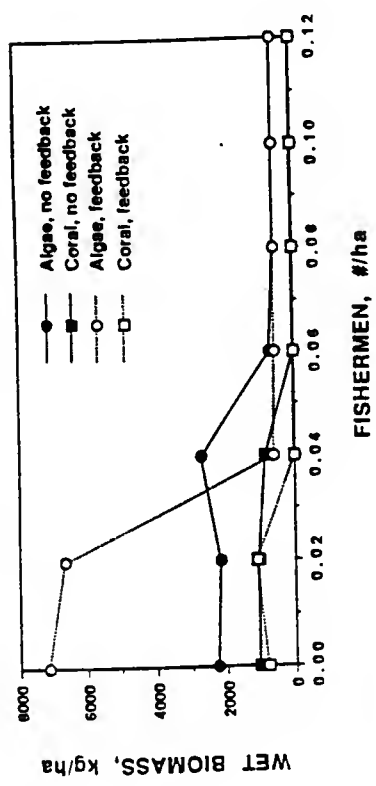
maintained at a high level. Algal biomass is unrealistically high for the simulation having a feedback from sea urchins to algae (Fig. 59).

DISCUSSION

Disturbed Hierarchy on East African Reefs

Typical of coral reefs throughout the world, East African reefs have developed a complex limestone structure with a large species diversity. Measurements in this study show a hierarchical organization in which larger fishes, at higher positions in energy hierarchy exert controls that help maintain ecosystem diversity and processes. Both the model and the field data suggest that the removal of top carnivores can dramatically influence the rest of the community. The field data describe two extreme states (i.e. fished versus unfished) while the model allows for comparisons of various gradations of fishing intensity. Both suggest a transition from a fish-dominated to an urchin-dominated grazing system dependent on the level of triggerfish (invertivores) and their ability to directly and indirectly affect guilds below them.

Emergy Signature and Dominant Components

The ecosystem's Emergy signature (Table 1) is the set of energy sources contributing and affecting ecosystem processes. Those

species and processes that are well adapted should prevail and utilize the main kinds of energy sources. Large ocean currents energies flow adjacent to coastal reefs, but the energy absorbed per unit of reef area is apparently greater from waves. Most wave energy is dissipated on the reef while a smaller fraction of current energy is absorbed.

Emergy theory (Odum 1983) hypothesizes that the effect of a resource is proportional to the energy used to create it (i.e. Emergy). The kinetic energy of waves and currents provides a constant supply and flushing of carbon (HCO_3^-), oxygen, zooplankton, phytoplankton, dissolved nitrogen, phosphorus and other elements which may be important for reef production processes. Studies (Kinsey 1977, Hatcher 1981) have shown that reef lagoons are less productive than reef crests and edges. This has been attributed to reduced water movements in reef lagoons due to decreased waves and currents behind the reef platform. Most research on reef production has focused on sunlight (Larkum 1983) or nutrients such as nitrogen (Hatcher and Larkum 1983, Williams and Carpenter 1988) as potential limitations of reef production. In the future, it may prove fruitful to experimentally study the role of waves, currents and water movement in production processes in order to determine the importance of these physical energies in primary production. In reef microcosm studies, Adey (1987) found hydrodynamic factors critical for primary production.

Energy flow along the coast is highly seasonal with the maximum energy flows and emergy (i.e. Fig. 6) occurring during the southeast monsoons (May to September). During this period the air

mass is moving north towards the Intertropical Convergence Zone situated over Asia (McClanahan 1988). This movement of air creates the strongest currents and waves. Benthic algal biomass peaks during this time (Moorjani 1978). The causes of this are not entirely clear (McClanahan 1988), but may be a combination of high physical energies, increased water clarity, reduced temperatures and herbivory during the southeast monsoon. During the northeast monsoon (September to May) maximum solar energy occurs and water and air movements are reduced. During this period pelagic algae reaches its maximum biomass (Bryceson 1982) which results from water column stability that allows the nitrogen fixing algae *Oscillatoria erythraea* to stay near the water surface and photosynthesize. Seasonality creates periodicity in the optimal conditions for benthic and pelagic systems which allows species with linkages between systems to benefit from both conditions on a seasonal basis. This results in the observed seasonal recruitment patterns of benthic organisms.

Transformity and Hierarchical Position

Solar transformities indicate the hierarchical position of the reef components (Table 2). This measure represents a guilds position in the food web, but also included (Table 1) is non-living turbulence which supports the production process. Among living components triggerfish (invertivores) and piscivores have the highest transformities, followed by herbivorous fish, sea urchins, coral and

algae. The transformity of the fisheries species (around 1E+8) is high in comparison with other meat production systems (Brown *et al.* in press). This suggests that many carnivorous species may be too valuable as reef control agents to be used as meat. Coral reefs may be inefficient fish production systems for humans as a great deal of the production is consumed internally. High transformities suggest their greatest value may be for their roles in biotic control, tourism, and shoreline protection. Feeding lower on the trophic chain (i.e. herbivorous fish and sea urchins) may be more beneficial to the coral reef and its long-term production.

Territory, Turnover Time and Control Windows

Hierarchies of nature can be represented by a graph of replacement time as a function of spatial territory (Fig. 60). Small things turnover rapidly whereas larger ones have larger territories and are made and replaced more slowly. The main components of the East African reef placed in such a graph indicate the components' time scale and their position in the hierarchy. Items to the upper right can affect the system over the longer time scale while those on the lower left have impacts on the short time scale.
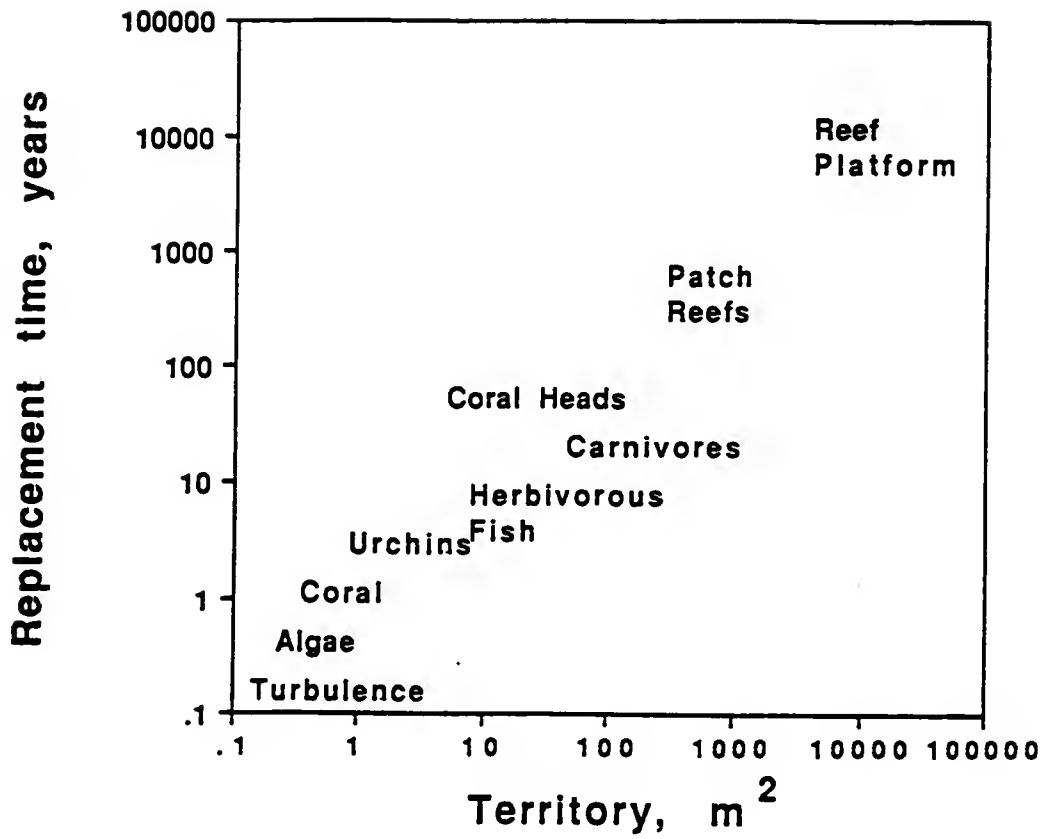
Fig 60. Graph of replacement time and territory of the major studied coral reef components.

Hierarchical role of calcareous reef structure

The fisheries model included each of the above components and determined that, for the time scale of investigation, the larger reef structure was not important in controlling production processes. Yet, on the longer time scale the reef structure may have an important feedback effect. As indicated by Figure 23 large coral heads and the reef structure itself have a high position in the hierarchy and represent those corals which have survived the longest and have received a long period of work by natural processes. The simple model of Figure 61 shows the way calcareous structure is a type of hierarchical control since it supports, facilitates, and amplifies the other reef processes (ie. waves, currents, sunlight) required to generate reef production processes. Preliminary simulations with this model (not included) indicated that, in initial stages of reef development, reef structure had an effect on growth, but once the structure is well developed its large storage makes its effect almost constant. Identifying factors that control ecological processes may largely be a function of defining the time scale or window of interest.

Hierarchical Patterns of Space and Species Abundance

Analysis of rank-abundance relationships and body size for the total sea urchin assemblage suggest that smaller species are more
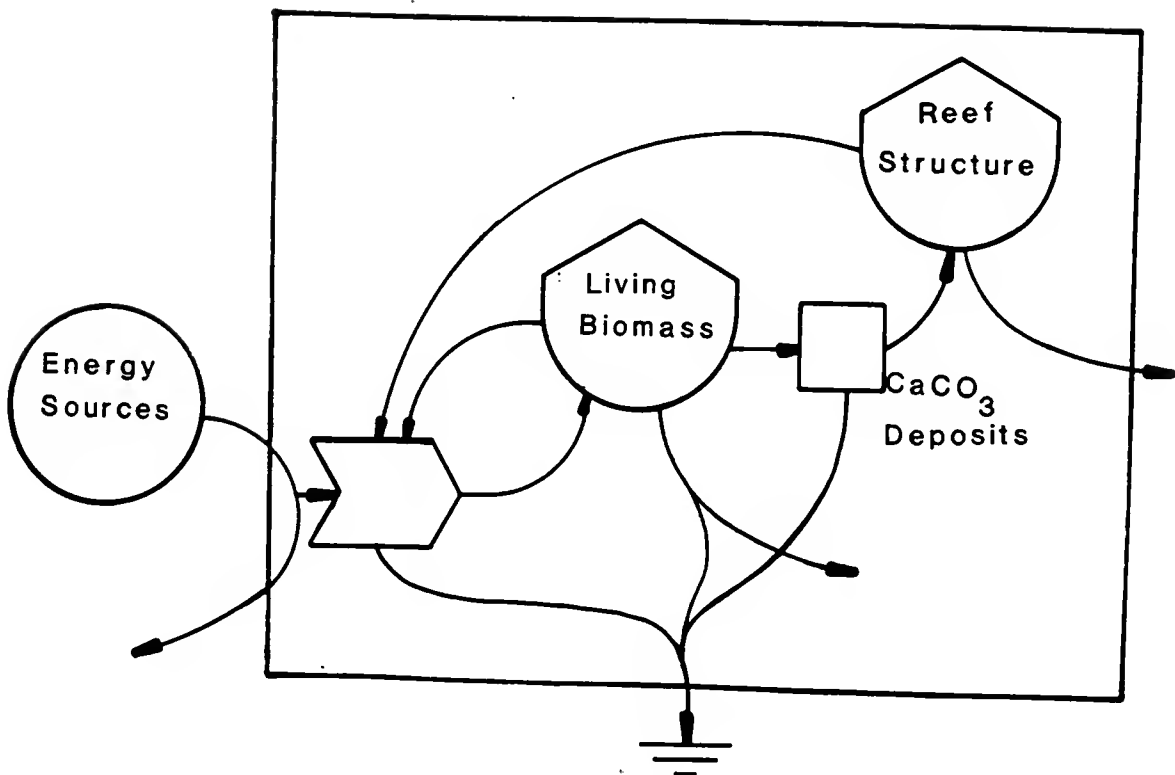
Fig 61. The feedback role of reef structure in the production process of a coral reef.

abundant than larger species. Further, there appears to be a hierarchical distribution of topographic complexity (i.e. many small crevices and undulation and few large crevices or undulations). Body size is important in spatial resource utilization and therefore species abundance should be related to spatial properties of reef substrate. Smaller species should be more abundant than larger species due to the increased space or spatial refuge available to them. A study of insects by Morse *et al.* (1985) found that smaller species were more abundant than larger species and they attempted to explain this observation with a fractal model of space (Mandelbrot 1977). The fractal geometry of some landscapes including coral reefs (Bradbury *et al.* 1984) are such that space increases with smaller lengths of measurement. Niche partitioning research should focus further on the relationship between body size and spatial properties of the landscape.

Mechanisms of Hierarchical Control

Predator Control of Sea Urchins

The strong negative correlation between experimental predation rates and sea urchin density (both are independent variables) suggests that predation acts as an important control on the sea urchin's community structure. Balistids, particularly *Balistaphus undulatus* and *Rhinecanthus aculeatus*, are the principal predators. Results support direct observations on the consumption of

experimental sea urchins in Malindi where *B. undulatus* consumed >90% of the predated sea urchins placed in the lagoon (McClanahan and Muthiga 1989). In protected reefs *B. undulatus* were typically observed in deeper (1 to 2 m) coral outcrop areas. Unprotected areas contained similar habitat and therefore fishing may be the cause of *B. undulatus* absence rather than the lack of suitable habitat.

The sea urchin assemblage showed differences in species composition and abundance between reefs which can largely be attributed to predation. Protected reefs had a distinct assemblage composed primarily of adult *Echinostrephus molaris* and *Echinothrix calamaris* and juvenile *E. mathaei*. The absence of other species is presumably due to high predation in these reefs. *E. molaris*, the most common species reaching adult size, may be able to persist because it inhabits deep narrow (about 10 cm x 3 cm) burrows (Campbell *et al.* 1973). The rarer *E. calamaris* has a large body size (adult test lengths are about 20 cm) and spines which may reduce predation rates. The existence of *E. mathaei* recruits in protected reefs suggests that they settle from the plankton and could potentially colonize protected reefs if predators were absent.

The existence of additional species in unprotected reefs, principally *D. savignyi, D. setosum* and *T. gratilla*, and increased densities of all sea urchin species can be attributed to decreased predation intensity by balistids. Yet, as predation intensity decreases *E. mathaei* becomes increasingly dominant which appears to result in competitive exclusions and localized extinctions. Experiments on *E. mathaei* showed intra- and inter-specific agonistic behavior apparently causing localized exclusion of the larger

Diadema species. This same interference behavior may affect other species as well, and higher *E. mathaei* settlement rates may give it a competitive advantage.

Species Diversity Control by Selective Consumption (Compensatory Mortality)

As suggested in Figure 3b consumers can influence the state of an ecosystem by selection processes. Experiments of predation on the dominant sea urchins suggest coexistence mechanisms facilitated by consumer preferences. The three most intensely studied species, *E. mathaei, D. savignyi* and *D. setosum* form a morphological and behavioral continuum related primarily to predator avoidance, secondly to intraspecific competition and lastly interspecific competition. The species different body morphologies allow them to utilize different size crevices which occur due to the reef's variable topography (Fig. 62). *E. mathaei* burrows into the reef substrate which allows it some self-reliance in crevice availability. *Diadema*, on the other hand, use larger crevices created by the physical and biological erosion of the reef. The small body size and crevice sizes of *E. mathaei* assure that it will not compete with *Diadema* at high predation rates as *Diadema* crevices are too large to insure *E. mathaei* sufficient protection from predation. Conversely, *E. mathaei* crevices are too small for *Diadema* to enter. Yet, at low predation rates *E. mathaei* has the potential to expand its distribution and compete with *Diadema*. Similar dietary preferences indicate that the species
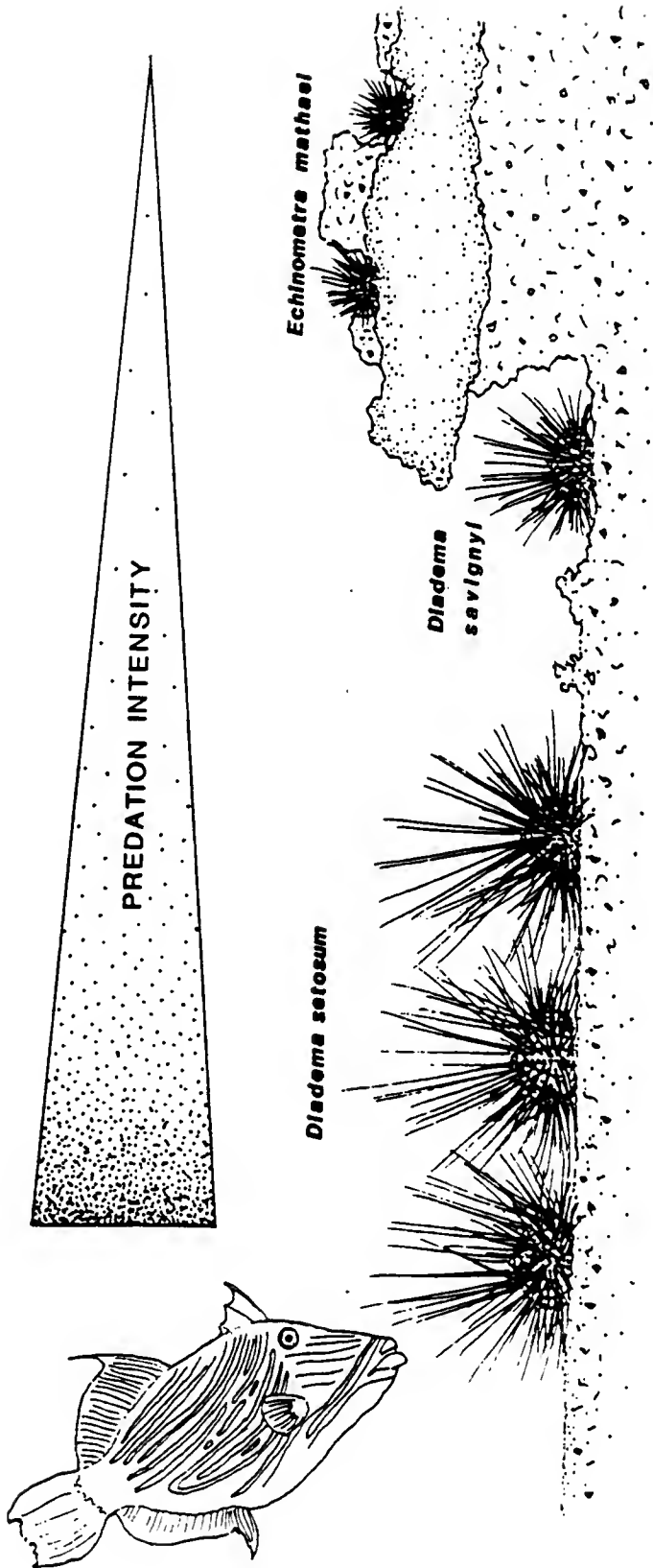
Fig. 62. Drawing of the relationship between the microspatial habitats of the three sea urchins and the degree of predation intensity relative to *Echinometra mathaei*.

have the potential for food resource competition, but because of predation, competition is more likely to be for predator-free space (Sih *et al.* 1985) than for food. The importance of competition differs between reefs primarily as a function of predation intensity.

Control of Competition Between Sea Urchins and Herbivorous Fish

Data presented here and collected in other regions (Hay and Taylor 1985, Foster 1987, Morrison 1988, Carpenter 1990) suggest that sea urchins are superior competitors for benthic algae and space in the absence of predation. Implications of the modelling are that, despite the lower consumption and turnover rates of sea urchins, they are able to reduce algal biomass below levels at which herbivorous fish can feed. This appears to be the reason for their superior competitive ability in the absence of predation. A literature survey of algal biomass in urchin and fish dominated reefs (Table 24) supports the suggestion that urchins graze algae to a lower level than herbivorous fish. Sea urchins appear to be able to ingest large quantities of reef substrate with their food which reduces algal biomass and subsequently increases reef substrate erosion. Low rates of algal consumption by sea urchins allows sea urchins to reach high biomass values.

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Table 24. A comparison of reported literature algal biomass values for comparisons between fish and sea urchin dominated grazing areas. Data reported in dry but not decalcified weights. Adjusted numbers assume decalcified weight is 1/5 dry weight (Hughes et al. 1987). n.g. = data not given, dw=dry weight, ww=wet weight

Reference	Location	Biomass gdw/m²	Herbivore Abundance
Fish Dominated Reefs			
Odum and Odum (1955)	Eniwetok	320	9 gww/m²
Bakus (1967)	Eniwetok	124	n.g.
Hatcher (1981)	One Tree Reef	90-190	5-20 gww/m²
Foster (1987)	Panama	175	n.g.
Urchin Dominated Reefs			
Hughes et al. (1987)	Jamaica	7.5-64.3	87.5-99.5 I/m²
Sammarco et al (1973)	St. Croix	11.88	2-6 I/m²
Carpenter (1981)	St. Croix	15-30	13-14 I/m²
Levitan (1988)	St. John	2.2	13 I/m²
Foster (1987)	Panama	50	2-3 I/m²

Control of Substrate Cover and Production

Substrate variables suggest distinct and consistent differences dependent on the dominant herbivore as indicated by differences between protected and unprotected reefs. Differences between these categories may be attributable to i) a reduction in finfish, ii) an increase in sea urchins or iii) a combination of both changes. Sea urchins are major bioeroders of coral reef substrate in many regions (Ogden 1977, Glynn *et al.* 1979, Scoffin *et al.* 1980, Hutchings 1986, Downing and El-Zahr 1987 Birkeland 1988) and their bioerosion rates are at least an order of magnitude greater than those of finfish grazers such as parrotfish (Birkeland 1988). Consequently, the observed reduction in topographic complexity with increasing sea urchin density may be because of more bioerosion. The greater algal turf cover and subsequent lower substrate diversity suggest that sea urchins are exposing bare calcium carbonate substrate and reducing substrate cover types such as coral and calcareous algae which are then quickly colonized by algal turf.

The experimental determination of *E. mathaei* reef substrate erosion rates are similar to most other reported values (Birkeland 1988). Field measurements and the model suggest that high bioerosion rates on unprotected reefs will result in a loss of coral heads and their structure.

E. mathaei gut studies show that the quantity of food (gut fullness) decreases with increasing densities. This suggests that algal turf biomass is decreasing with increasing sea urchin densities.

Studies on coral reef algal turf indicate that gross production will decrease with decreasing biomass (Hackney and Sze 1988) and net production will occur at some intermediate level of grazing (Carpenter 1981). Grazing appears to have a positive feedback on algal turf (Carpenter 1988), perhaps through increased nitrogen cycling (Williams and Carpenter 1988). Consequently, reefs' gross and net production will be affected by sea urchin biomass. Reefs with high sea urchin densities (i.e. Kanamai and Diani) will have a reduced gross and perhaps reduced net production. It remains unknown, but of interest, what the differences in primary production are between fish-dominated and sea urchin-dominated reefs.

Overgrazing and Starvation Without Hierarchical Control

Gut content analysis indicated that *E. mathaei* takes in less food and more inorganic substrate with increasing population density. Populations begin to show signs of starvation at high densities. The larger Aristotle's lantern at high densities, also found by Black *et al.* (1982, 1984), implies that urchins are investing more energy into their feeding apparatus to compensate for reduced food availability (Ebert 1980). This suggests that agonistic behavior will not regulate *E. mathaei* population densities in the absence of predation.

Control by Recycle and Positive Reinforcement

Control of ecosystem structure and processes is attributable to multiple pathways of interaction (Fig 3). Nutrient recycle (Fig 3c) is a commonly accepted form of consumer control. Sea urchins have nitrogen fixing gut symbionts which increase the nitrogen content of their feces which appears to accelerate algal production (Williams and Carpenter 1988). Many foraging fishes congregate on coral reefs while resting, digesting and defecating. This behavior significantly stimulates coral growth (Meyer and Schultz 1985). Carpenter (1988) found a significant drop in algal production following the mass mortality of *D. antillarum* in the Caribbean suggesting pathways of reinforcement between the grazer and its producer.

Simulation models with feedback reinforcements suggest that feedbacks can increase the biomass and production of primary producers but the effect on higher trophic levels is dependent on trade-offs between energy expended and gained. In simulated models, feedbacks did not affect consumers unless the consumer expenditure was small (i.e. <5% of energy consumption) and the feedback effect on production large (>20% of baseline production). Consequently, consumers may not develop feedbacks unless it is possible to fullfill the above criteria. Feedbacks would not be expected to develop where there is not net gain of energy to the consumer. Since energy is lost thermodynamically due to interactions and transformations along the food chain, feedback effects should not develop unless the effect is greater than thermodynamic losses.

Additionally, feedback models were more sensitive to fishing perturbations. Perhaps feedbacks will develop in stable ecosystems where feedback effects will benefit species expending the energy and where feedback developments are unlikely to destabilize the ecosystem when perturbations are present.

Feedbacks and Compensatory Mortality

Feedback and compensatory are two potential methods of consumer control. Feedback models emphasize the energy expenditure of a consumer that increases production at lower levels. Compensatory mortality emphasizes choices made by consumers. Making choices requires an energy expenditure through knowing and processing information about the environment. Organisms expend energy travelling within their territories and while processing information through the organisms senses and brain. They select prey which maximize their net energy return by minimizing expenditures and maximizing gross gains. These choices may increase production of lower trophic levels if they reduce the abundance of less productive individuals (i.e. nonproductive, ill, senescent, organisms outside their optimal niche) and therefore allow energy to be used by more productive individuals (Slobotkin 1969). Predators which feed on low-productivity individuals may be using an optimal foraging strategy by reducing the energy they expend in pursuing and handling prey. Consequently, feedbacks and

compensatory mortality may be complementary processes one emphasizing choices, the other energy expended in predation.

The maintenance of the coral reef appears to result from a number of compensatory or feedback processes. It has already been pointed out that the maintenance of species diversity requires predation on the top competitor which also has the highest intrinsic growth rate. The maintenance of coral, its deposition of calcium carbonate and the resultant reef structure requires herbivores and their preference for fast-growing fleshy algae. Finally, the persistence of herbivorous fish and reef structure appear to depend on the predatory behavior of invertivores. The lack of one or a combination of these functional groups could potentially cause major shifts in the reef's structure. This hypothesis and model simulations suggest that the reef has the potential for multiple equilibria dependent on the presence and abundance of these trophic groups.

Pristine coral reefs from disparate world regions appear to share similar attributes (i.e. coral cover, calcium carbonate structure, high productivity and species diversity) and the reef structure is one of the oldest and persistent communities on earth (Newell 1972). This persistence is not a result of a static equilibrium between species but rather interactions which allow the persistence of different life history strategies through compensatory or feedback processes. Compensatory interactions and predation are similar to negative feedback interactions in the sense that they keep components bounded within limits.

Resolution of Concepts of Population and Systems Ecology of Reefs

Controversies between population and systems ecology concepts often involve the particular window of focus. If only components and mechanisms at the population scale are viewed hierarchical controls from higher levels such as hydrodynamic energy flows and "disturbances" are often ignored. If only larger scale phenomena and their feedbacks are viewed, population level phenomena are often ignored. For example, my field data indicates that coral reefs can have different equilbrium states dependent on the intensity of interspecific interactions even though both systems receive the same energy flow and disturbance regimes. If viewpoints and models cover at least two or three orders of magnitude in an energy hierarchy then differences over matters of importance can be resolved.

Large scale phenomena depend on energy transformations of small scale phenomena, but the small scale is controlled by larger scale processes with longer time constants, greater flexibility and energy density. These large-scale processes can disturb or interact with small-scale phenomena to change biotic interactions between species, to recycle stored nutrients and stimulate production processes. Both scales are necessary for any coherent theory of nature.

Effects of Overfishing

Overfishing removes part of the upper hierarchy of the ecosystem that controls the rest of the ecosystem. In East Africa, overfished reefs and reefs protected from fishing provided a large scale experiment for study of the effects of fishes as hierarchical controls.

Reorganized System of Overfished Reefs

The two food chain pyramids in Figure 29 contrast the normal with the overfished reefs. Without the larger, slower controls, overfished ecosystems increased in variability and were dominated by rapid population changes of smaller components (algae and urchins) with losses of productivity, diversity and structural complexity. Distinct differences were observed in fish fauna's absolute and relative density, family composition and trophic importance. Fish had consistently reduced sizes in unprotected reefs and an increase in the relative abundance of the less preferred food-fish families (i.e. small Labridae and Pomacentridae). Additionally, although not quantified, fish species diversity and species richness appeared reduced in unprotected reefs. In contrast sea urchin species richness was highest on unprotected reefs. The loss of finfish species richness appears to be partially compensated for by sea urchins which have similar ecological roles but I suspect that the total species richness is reduced on unprotected reefs. The total

urchin guild is smaller (i.e. 10 to 12 species) than the finfish assemblage (i.e. 200 to 400 species).

Results of this survey suggest that nearshore Kenyan reefs, like Jamaican reefs (Koslow *et al.* 1988), are susceptible to over- fishing. A lack of larger size classes and reduced densities of smaller size classes in fished reefs, particularly among preferred food-fish families, suggest that fishing is beyond its maximum sustainable yield. Fished reef lagoons appear to be inhabited mostly by small Labridae, Pomacentridae, Holocentridae, Apogonidae and Ostraciidae which are among the less preferred food-fish families. There is a notable paucity of the preferred Scaridae, Siganidae, Lutjanidae, Serranidae and Lethrinidae in fished reefs. Family composition differences in Kenyan reefs were similar to changes caused by fishing within Jamaican reefs (Koslow *et al.* 1988). This suggests similar overfishing trends in coral reefs from disparate regions of the world.

Secondary and "indirect" effects of fishing appear to be having additional adverse effects on the fish fauna. Reduced densities of some less preferred food-fish families such as the Pomacentridae and Chaetodontidae in unprotected reefs suggest some secondary effects which may not be directly attributable to fishing. One might suspect actual density increases in some of these species due to reduced predators and competitors (Koslow *et al.* 1988). There were also disproportionately lower densities of herbivorous fish, particularly the Scaridae and Acanthuridae, in fished reefs compared to other trophic groups. Other undetermined fish herbivores such as the Blennidae and Gobiidae probably contributed only a small percentage

to the herbivore biomass. A disproportionate increase in fishing effort focused on these species may be insufficient to explain this decrease particularly for the Acanthuridae which contains some species of lower food preference.

The strong negative relationship between sea urchin density and herbivore fish abundance suggests that sea urchins have competitively excluded herbivorous fish. Hay and Taylor (1985) experimentally removed urchins from a reef in the Caribbean and found an increase in herbivorous fish shortly afterwards. Additionally, mass mortality of *Diadema antillarum* within the Caribbean in 1984 resulted in the rapid return of herbivorous fish populations in St. Croix (Carpenter 1990) and Jamaica (Morrison 1988). The competitive exclusion of herbivorous fish by sea urchins combined with overfishing may have caused spatial displacement and localized extinctions of fish herbivores.

It remains debatable whether all differences can be attributed to fishing, as the necessary experiments and long-term monitoring have not been undertaken. Alternative explanations might include intrinsic site differences independent of fishing. For example, the protected reefs had greater topographic complexity and coral cover than unprotected reefs which has been shown to effect coral-reef fish (Luckhurst and Luckhurst 1978, Bell and Galzin 1984, Bouchon-Navaro *et al.* 1985). But, there was less effect between reef topographic complexity and fish density in unprotected reefs.

Reduced substrate complexity and coral cover in fished reefs is more likely to be explained by high sea urchin densities and associated bioerosion rates in unprotected reefs rather than intrinsic site differences. Consistently reduced fish sizes and the increased relative abundance of less preferred food-fish families (i.e. small Labridae and Pomacentridae) indicates differences attributable to fishing rather than site differences. Differences in sea urchin abundance and diversity might also be attributed to intrinsic site differences but observations by local residents (Simpson B. and Abudi M. personal communication) suggest that *E. mathaei, Diadema* spp. and *Tripneustes gratilla* were previously more common on Malindi and Watamu reefs prior to and shortly after their protection. Site differences may account for some variation but differences between protected and unprotected reefs are most likely attributable to fishing.

Responses of Fisheries Model to Overfishing

Model and field results support the contention that removing fish can have impacts on the whole ecosystem and can interfere with competitive and compensatory interactions which structure the reef as well as the long-term fisheries productivity. In order to develop coral reef fisheries management policies the internal dynamics of the coral reef community must be understood. Single or even multiple-species fisheries models may be insufficient in predicting long-term fisheries yields as unexpected changes of other unutilized species,

resulting from removal of their predators or competitors, may interfere with production of targeted fisheries species. Consequently, ecosystem models (ie. Grigg *et al.* 1984) which rely on an understanding of the internal community structure and dynamics may hold the most promise.

The model presented here indicates that fishing will have many indirect effects on the major reef components. Any amount of fishing will affect reef processes as algal and coral are affected even at low levels of fishing. Additionally, when all fish components are fished, major reef changes occur before the projected maximum sustained yield of fish catch.. In fact, the model predicts that the reef will be converted into a "sea urchin barren" before maximum sustained yield is reached.

Hierarchical Role in Maximizing Productivity

Energy has been suggested as a currency for nature but unless energy is transformed into products its value to a species or a system is limited. Transformation of energy is one basis for hierarchy and a basis for the production of useful energy products. The maximum power principle suggests that hierarchical patterns result during self-organization because these patterns cause greater useful productivity (greater intake of resources, more transformation into products, and more utilization of products to maximize efficiencies of conversion). Mechanisms by which consumers maintain the production process, namely material recycle, feedback reinforcement

and compensatory mortality (Fig. 3) are critical to the maintenance of ecosystem structure, diversity and productivity. When top levels of the hierarchy are missing, energy is not being transformed into products that amplify production, diversify production or maintain stability of function. Management of coral reef and other systems may benefit from recognizing the various roles of these hierarchical feedbacks.

Recommendations for Reef Management

Humans and their economy are high in the hierarchy, generally in a position to interact and control reef structure and processes. Also, components high in the ecosystem's hierarchy (i.e. fishes and reef structure) are what interest and impact humans. By controlling these top components, it is possible to indirectly manage the reef. A human partnership with nature has been called ecological engineering.

A reef can be managed for multiple uses; most importantly these include fisheries yields, diversity and shoreline protection. Considerations, apart from maximum sustained fisheries yield must be considered. For example, instead of managing a coral reef for maximum sustained yield one might manage a reef to insure that reef accretion rates are greater than present sea level increases (about 2.3 mm/yr, Buddemeier and Smith 1988). Management of an ecosystem requires a knowledge of the time and spatial scale of human impacts. Factors both low and high in the hierarchy (Fig. 60)

are difficult to control by humans. Consequently, by controlling components in the middle of the hierarchy (i.e. fish) other factors of human interest may be controlled indirectly.

Further, fishermen might use principles of hierarchical feedback such as compensatory mortality. Compensatory fishing would be achieved by selectively removing the most abundant fish species and leaving rarer species. Alternatively, fishermen might reduce piscivorous predators and then focus on their prey (Grigg *et al.* 1984). Models suggest that removing only piscivores will result in low levels of fisheries production. But, removing piscivores and focusing on herbivorous fish results in the greatest yields and allows the most intense fishing. This method also maintains reef structure and accretion rates. Fishing invertivores is the most detrimental fishing technique unless fishing is below the level at which sea urchin populations dominate herbivorous fish. In general, if a predator feeds on a prey which has little economic value or is destructive to coral reefs (i.e. sea urchins) then these predators should be left unfished.

Perhaps interactive management is the most acceptable management technique (Walters 1986). This method would involve measuring certain ecosystem indicators (i.e., the density of sea urchins or algal biomass) and stopping fishing for certain periods when values differ from a predetermined threshold. This management strategy requires rotating reserves which would allow some reefs recovery periods while fishing others. This method could be developed based on a statistical design intended to determine fishing impacts. The frequency and duration of fishing pulses in

reserves remains a subject requiring additional research but may be regionally specific and dependent on recruitment and growth rates of important species.

If protection is supplied so that coral reefs can retain their larger populations and full diversity, a maximum diversity ecosystem develops, one of great value for conservation, aesthetics, tourists, and the maintenance of clean coastal waters. Because of the intricate coral reef network, park policies allowing fishing may be inappropriate for coral reefs. Top-level carnivores may have a more important role in maintaining diversity and in teaching students about ecosystems and natural beauty than their minor food contribution.

Summary

Data presented in this dissertation are supportive of a top-down perspective for coral reefs (Grigg *et al.* 1984) where species and populations are controlled by their consumers. Changes at top trophic levels may have cascading effects on lower levels which include species composition changes, and reef processes such as the calcium carbonate balance, gross and net production. The major change between protected and unprotected reefs is the inclusion of human predators in unprotected reefs which adds an additional

consumer and trophic level to the reef. Predation on triggerfish by humans appears to have a major influence on the rest of the community to the extent that fished reefs are essentially different ecosystems from unfished ecosystems (Aronson and Harms 1985). In fished ecosystems reef production is routed through sea urchins opposed to herbivorous fish in unfished reefs. This has unexpected affects on reef primary production and the calcium carbonate balance. Triggerfish are neither abundant or a preferred prey of local fishermen but their removal has disproportionate consequences. Seemingly unimportant decisions such as whether or not to consume a particular species (ie. triggerfish) can have a major influence on the ecosystem. In the absence of predation energetic limitations and starvation ultimately regulate sea urchin populations. The lack of competition, predation or disease may eventually led to a local population collapse associated with the self-induced resource destruction of the coral reef hard substrate ecosystem.

From an economic-anthropogenic viewpoint coral reefs 1) provide aesthetic beauty 2) protect the shore and beach from erosion, 3) support species diversity with stored information of millions of years of evolution which attracts tourism 4) provide food in the form of fish and invertebrates, and 5) precipitate 50% of the worlds calcium carbonate. Consequently, the organization of the coral reefs can have important implications to the world's global energy budget, nutrient cycling and to the support of tropical coastal economies. Research results presented here on East African coral reefs suggest that all of the above ecosystem services can be affected by fishing.

COMPUTER PROGRAM OF TURNOVER AND YIELD

```
REM THIS PROGRAM VARIES THE TURNOVER TIME OF THE
CONSUMER
8    DIM  x(20),d(20),Z1(20),z2(20),Z3(20),Z4(20),Z5(20),z6(20),Z7(20)
10 REM CORAL REEF
20 REM MACINTOSH
25 CLS
xsize=460
ysize=200
yone=ysize/4
ytwo=ysize/2
ythree=ysize*.75
ienter=14
30 LINE  (10,0)-( xsize,  ysize),,B
33 LINE  (10,  yone)-(xsize,yone)
34 LINE  (10,  ytwo)-(xsize,ytwo)
36 LINE  (10,ythree)-(xsize,ythree)
startrun:
PC=.05
TV=0
LOCATE ienter,1:INPUT "enter dt:";dt
```

```
LOCATE ienter+3,1:INPUT "FISHERMEN/HA"; M

LOCATE ienter+6,1:INPUT "carbon/m2:"; gc

IF dt=0 THEN STOP

OPEN "CLIP" FOR OUTPUT AS #1

TURNOVER:

TV=TV+.01

M=0

IF M=0 THEN GOTO INITIALIZE

FISHING:

M=M+.2

INITIALIZE:

ins=43835!

a=1000

f=500

p=25

REM THIS VERSION OF THE MODEL INCREASES ALGAL BIOMASS TO
8500KG/HA

REM MAX CORAL BIOMASS 4800 KG/HA

REM GRAMS CARBON X2 = DRY WEIGHTX 2.5 =WET WEIGHTX 10
=KG/HA

   K=(gc*2*10*2.5)/(8500*4383.5)

   K0=(43835!*.9)/(8500*4383.5)

   K1=(gc*2*10*2.5)/8500

 REM FISH CONSUME 22% AND URCHINS 4.5% OF BODY WT. AT MAX.
DENSITY

REM MAX HERB FISH DENS 150 KG/HA, URCHINS 5000KG/HA

REM DRY WEIGHT IS 40% OF WET WEIGHT
```

```
REM ALGAE IS 4.7 % OF MAX. AT FULL HERBIVORY

  K5=  (500*PC)/(500*8500*.047)

  K7=  (500*PC*TV)/(500*8500*.047)

  K8=((500*PC*TV)/500)

  x=0

T0=4

  nd=7:z2=dt/2:z6=dt/6

x(1)=a:x(2)=c:x(3)=u:x(4)=f:x(5)=t:x(6)=p:x(7)=h

a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)

starttime:

330  PSET  (x/T0+10,yone-a/200)

370  PSET  (x/T0+10,  ytwo-f/20)

380  PSET  (x/T0+10,  ythree-p/2)

TME=x/365

LOCATE 17,17: PRINT "time, m, TV, a, f, :"; TME; M; TV; a; f

GOSUB model

 FOR I = 1 TO nd:Z1(I) = d(I):Z7(I) = x(I):z2(I) = x(I) + Z1(I) * z2:x(I) =
z2(I): NEXT

 tim= Z9 + z2

 GOSUB model

 FOR I = 1 TO nd:Z3(I) = d(I):Z4(I) = Z7(I) + Z3(I) * z2:x(I) = Z4(I): NEXT

 GOSUB model

 FOR I = 1 TO nd:Z5(I) = d(I):z6(I) = Z7(I) + Z5(I) * dt:x(I) = z6(I): NEXT

 tim= Z9 + dt

 GOSUB model

 FOR I = 1 TO nd:x(I) = Z7(I) + (Z1(I) + 2 * Z3(I) + 2 * Z5(I) + d(I)) * z6:
NEXT
```

```
a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)

 x=x+dt

IF  x/T0<xsize-10  THEN  GOTO  starttime

PRINT #1, USING "######.### "; PC; TV; f; M; CA

IF M<2 THEN GOTO FISHING

IF TV<.05 THEN GOTO TURNOVER

CLOSE #1

STOP


REM  model  goes  here

model:

a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)

REM CALCULATING

 RI=ins/(1+a*K0)

 d(1)=a*RI*K-a*K1-a*f*K5

 d(4)=f*a*K7-f*K8-M*f*K16

CA=(M*f*K16)*365

RETURN
```

APPENDIX B

COMPUTER PROGRAM OF CONSUMPTION AND YIELD

```
REM EXPLORES THE EFFECTS OF CONSUMPTION RATES ON BIOMASS
AND FISH CATCH
8    DIM  x(20),d(20),Z1(20),z2(20),Z3(20),Z4(20),Z5(20),z6(20),Z7(20)
10 REM CORAL REEF
20 REM MACINTOSH
25 CLS
xsize=460
ysize=200
yone=ysize/4
ytwo=ysize/2
ythree=ysize*.75
ienter=14
30 LINE (10,0)-( xsize, ysize),,B
33 LINE (10, yone)-(xsize,yone)
34 LINE (10, ytwo)-(xsize,ytwo)
36 LINE  (10,ythree)-(xsize,ythree)
startrun:
PC=.05
LOCATE ienter,1:INPUT "enter dt:";dt
LOCATE ienter+3,1:INPUT "FISHERMEN/HA"; M
```

```
LOCATE ienter+6,1:INPUT "carbon/m2:"; gc

IF dt=0 THEN STOP

OPEN "CLIP" FOR OUTPUT AS #1

CONSUMPTION:

PC=PC+.05

M=1.5

IF M=0 THEN GOTO INITIALIZE

FISHING:

M=M+.075

INITIALIZE:

REM FISHERMEN=M & MT

ins=43835!

a=1000

f=500

p=25

REM   ALGAL BIOMASS IS 8500KG/HA

REM MAX CORAL BIOMASS 4800 KG/HA

REM GRAMS CARBON X2 = DRY WEIGHTX 2.5 =WET WEIGHTX 10

=KG/HA

  K=(gc*2*10*2.5)/(8500*4383.5)

  K0=(43835!*.9)/(8500*4383.5)

  K1=(gc*2*10*2.5)/8500

 REM FISH CONSUME 22% AND URCHINS 4.5% OF BODY WT. AT MAX.

DENSITY

REM MAX HERB FISH DENS 500 KG/HA, URCHINS 5000KG/HA

REM DRY WEIGHT IS 40% OF WET WEIGHT

REM ALGAE IS 4.7 % OF MAX. AT FULL HERBIVORY
```

```
K5=  (500*PC)/(500*8500*.047)

K7=  (500*PC*.05)/(500*8500*.047)

K8=((500*PC*.05)/500)

REM fishing coefficients

K16= .04

 x=0

 T0=4

319   nd=7:z2=dt/2:z6=dt/6

x(1)=a:x(2)=c:x(3)=u:x(4)=f:x(5)=t:x(6)=p:x(7)=h

a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)

starttime:

    PSET (x/T0+10,yone-a/200)

    PSET (x/T0+10, ytwo-f/20)

    PSET (x/T0+10, ythree-p/2)

TME=x/365

LOCATE 17,17: PRINT "time, m, PC, a, f, :"; TME; M; PC; a; f

GOSUB model

 FOR I = 1 TO nd:Z1(I) = d(I):Z7(I) = x(I):z2(I) = x(I) + Z1(I) * z2:x(I) =
z2(I): NEXT

 tim= Z9 + z2

 GOSUB model

FOR I = 1 TO nd:Z3(I) = d(I):Z4(I) = Z7(I) + Z3(I) * z2:x(I) = Z4(I): NEXT

GOSUB model

FOR I = 1 TO nd:Z5(I) = d(I):z6(I) = Z7(I) + Z5(I) * dt:x(I) = z6(I): NEXT

tim= Z9 + dt

GOSUB model
```

```
FOR I = 1 TO nd:x(I) = Z7(I) + (Z1(I) + 2 * Z3(I) + 2 * Z5(I) + d(I)) * z6:

NEXT

a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)

 x=x+dt

IF x/T0<xsize-10 THEN GOTO starttime

PRINT #1, USING "######.### "; PC; a; f; M; CA

IF M<2 THEN GOTO FISHING

IF PC<.3 THEN GOTO CONSUMPTION

CLOSE #1

STOP

REM model goes here

model:

a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)

REM CALCULATING

 RI=ins/(1+a*K0)

 d(1)=a*RI*K-a*K1-a*f*K5

 d(4)=f*a*K7-f*K8-M*f*K16

CA=(M*f*K16)*365

RETURN
```

APPENDIX C

COMPUTER PROGRAM OF ALGAE AND CORAL COMPETITION

```
REM  ALGAE AND CORAL COMPETITION
8    DIM  x(20),d(20),Z1(20),z2(20),Z3(20),Z4(20),Z5(20),z6(20),Z7(20)
10 REM CORAL REEF
20 REM MACINTOSH
25 CLS
xsize=460
ysize=200
yone=ysize/4
ytwo=ysize/2
ythree=ysize*.75
ienter=14
30 LINE (10,0)-( xsize, ysize),,B
33 LINE (10, yone)-(xsize,yone)
34 LINE (10, ytwo)-(xsize,ytwo)
36 LINE (10,ythree)-(xsize,ythree)
LOCATE ienter,1:INPUT "enter dt:";dt
IF dt=0 THEN STOP
OPEN "CLIP" FOR OUTPUT AS #1
INITIALIZE:
ins=43835!
```

```
a=1
c= 1
REM  MAX ALGAL BIOMASS IS 2090 0KG/HA(WET)
REM MAX CORAL BIOMASS 4800 KG/HA(WET)
REM  ALGAL GPP=10GC/M2/DAY = 500KG/HA/DAY(WET)
REM CORAL GPP=5000 KCAL/M2/YR =137 KG/HA/DAY(WET)
  K=500/(20900*4383.5)
  K00=(43835!*.9)/(4800*4383.5)
  K0=(43835!*.9)/(20900*4383.5)
  K1=500/20900
  K2=137/(4800*4383.5)
  K3=137/4800
 x=0
 T0=1
  nd=7:z2=dt/2:z6=dt/6
x(1)=a:x(2)=c:x(3)=u:x(4)=f:x(5)=t:x(6)=p:x(7)=h
a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)
starttime:
   PSET  (x/T0+10,yone-a/800)
   PSET  (x/T0+10, yone-c/200)
TME=X/365
LOCATE 17,17: PRINT "time, a, c, :"; TME; a; c;
 GOSUB model
 FOR I = 1 TO nd:Z1(I) = d(I):Z7(I) = x(I):z2(I) = x(I) + Z1(I) * z2:x(I) =
z2(I): NEXT
 tim= Z9 + z2
 GOSUB model
```

```
FOR I = 1 TO nd:Z3(I) = d(I):Z4(I) = Z7(I) + Z3(I) * z2:x(I) = Z4(I): NEXT
GOSUB model
FOR I = 1 TO nd:Z5(I) = d(I):z6(I) = Z7(I) + Z5(I) * dt:x(I) = z6(I): NEXT
tim= Z9 + dt
GOSUB model
FOR I = 1 TO nd:x(I) = Z7(I) + (Z1(I) + 2 * Z3(I) + 2 * Z5(I) + d(I)) * z6:
NEXT
a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)
x=x+dt
PRINT #1, USING "######.### "; TME; C; A
IF x/T0<xsize-10 THEN GOTO starttime
CLOSE #1
STOP
REM model goes here
model:
a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)
REM CALCULATING
 RI=ins/(1+a*K0)
 RF=ri/(1+c*K00)
 d(1)=a*RI*K-a*K1
 d(2)=c*RF*K2-c*K3
RETURN
```

APPENDIX D

COMPUTER PROGRAM OF SEA URCHIN AND HERBIVOROUS FISH COMPETITION

```
REM C OMPETITION BETWEEN HERBIVOROUS FISH AND SEA URCHINS
8   DIM  x(20),d(20),Z1(20),z2(20),Z3(20),Z4(20),Z5(20),z6(20),Z7(20)
10 REM CORAL REEF
20 REM MACINTOSH
25 CLS
xsize=460
ysize=200
yone=ysize/4
ytwo=ysize/2
ythree=ysize*.75
ienter=14
30 LINE (10,0)-( xsize,  ysize),,B
33 LINE (10,  yone)-(xsize,yone)
34 LINE (10,  ytwo)-(xsize,ytwo)
36 LINE (10,ythree)-(xsize,ythree)
LOCATE ienter,1:INPUT "enter  dt:";dt
LOCATE IENTER+3,1:INPUT "carbon/m2:"; gc
IF dt=0 THEN STOP
OPEN "CLIP" FOR OUTPUT AS #1
```

INITIALIZE:

pc=.22

pc1=.02

ins=43835!

a=1000

f=1

c=1

REM   MAXIMUM ALGAL BIOMASS IS 20900KG/HA (WET)

REM MAX CORAL BIOMASS 4800 KG/HA(WET)

REM GRAMS CARBON X2 = DRY WEIGHTX 2.5 =WET WEIGHTX 10

=KG/HA

  K=(GC*2*10*2.5)/(20900*4383.5)

  K0=(43835!*.9)/(20900*4383.5)

  K1=(GC*2*10*2.5)/20900

 REM ALGAE IS 4740 KG/HA (WET) AT FULL HERBIVORY FOR

HERBIVOROUS FISH

  K5= (500*PC)/(500*4740)

  K7= (500*PC*.01)/(500*4740)

  K8=((500*PC*.01)/500)

REM SEA URCHINS REDUCE ALGAE TO 612 KG/HA (WET)

  K9= (5000*PC1)/(5000*612)

  K10= (5000*PC1*.01)/(5000*612)

  K11=((5000*PC1*.01)/5000)

 x=0

 T0=12

  nd=7:z2=dt/2:z6=dt/6

x(1)=a:x(2)=c:x(3)=u:x(4)=f:x(5)=t:x(6)=p:x(7)=h

```
a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)
starttime:
330  PSET  (x/T0+10,yone-a/800)
370  PSET  (x/T0+10,  ytwo-f/20)
390  PSET  (X/T0+10,  YTWO-C/60)
TME=X/365
LOCATE 17,17: PRINT "time, f, c:"; TME; f; C
 GOSUB model
 FOR I = 1 TO nd:Z1(I) = d(I):Z7(I) = x(I):z2(I) = x(I) + Z1(I) * z2:x(I) =
z2(I): NEXT
 tim= Z9 + z2
 GOSUB model
 FOR I = 1 TO nd:Z3(I) = d(I):Z4(I) = Z7(I) + Z3(I) * z2:x(I) = Z4(I): NEXT
 GOSUB model
 FOR I = 1 TO nd:Z5(I) = d(I):z6(I) = Z7(I) + Z5(I) * dt:x(I) = z6(I): NEXT
 tim= Z9 + dt
 GOSUB model
 FOR I = 1 TO nd:x(I) = Z7(I) + (Z1(I) + 2 * Z3(I) + 2 * Z5(I) + d(I)) * z6:
NEXT
 a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)
 x=x+dt
TME=X/365
PRINT #1, USING "######.### "; TME; A; F; C
IF x/T0<xsize-10 THEN  GOTO starttime
CLOSE #1
STOP
REM MODEL STARTS HERE
```

model:

a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)

REM CALCULATING

RI=ins/(1+a*K0)

d(1)=a*RI*K-a*K1-a*f*K5-c*a*k9

d(2)=c*a*k10-c*k11

d(4)=f*a*K7-f*K8

RETURN

APPENDIX E

COMPUTER PROGRAM OF THE CORAL REEF ECOSYSTEM FISHERIES MODEL

```
REM TOTAL CORAL REEF-FISHERIES MODEL WITH REEF STRUCTURE
8    DIM  x(20),d(20),Z1(20),z2(20),Z3(20),Z4(20),Z5(20),z6(20),Z7(20)
10 REM CORAL REEF
20 REM MACINTOSH
25 CLS
xsize=460
ysize=200
yone=ysize/4
ytwo=ysize/2
ythree=ysize*.75
ienter=14
30 LINE (10,0)-( xsize,  ysize),,B
33 LINE (10,  yone)-(xsize,yone)
34 LINE (10,  ytwo)-(xsize,ytwo)
36 LINE (10,ythree)-(xsize,ythree)
LOCATE ienter,1:INPUT "enter dt:";dt
LOCATE ienter+1,1:INPUT "FISHERMEN/HA"; M
IF dt=0 THEN STOP
OPEN "CLIP" FOR OUTPUT AS #1
```

REM MAX ALGAL BIOMASS IS 2090 0KG/HA(WET)

REM MAX CORAL BIOMASS 4800 KG/HA(WET)

REM ALGAL GPP=8GC/M2/DAY = 400KG/HA/DAY(WET)

REM CORAL GPP=6500 KCAL/M2/YR=178 KG/HA/DAY(WET)

REM SURFACE AREA OF CORAL HEADS 3528M2/HA

K=400/(20900*4383.5*3528)

K00=(43835!*.9)/(4800*4383.5*3528)

K0=(43835!*.9)/(20900*4383.5*3528)

K1=400/20900

K2=178/(4800*4383.5*3528)

K3=178/4800

REM CORAL CALCIFICATION RATE

K4= .047

REM ASSUME ALGAE CONTRIBUTES TO REEF STRUCTURE AT 0.05X

CORAL

K24=.00235

REM HERB. FISH CONSUME 22% AND URCHINS 2% OF BODY WT. AT

MAX. DENSITY

REM MAX HERB FISH DENS 700 KG/HA, URCHINS 5000KG/HA

REM FISH REDUCE ALGAE TO 4740 KG/HA(WET) BUT *.5 TO ACCOUNT

FOR PISCIVORE IMPACT

REM URCHINS REDUCE ALGAE TO 612 KG/HA(DRY)

REM TURNOVER OF FISH ASSUMED 1%/DAY

REM TURNOVER OF SEA URCHINS ASSUMED 1%/DAY

K5= (700*.22)/(700*4740*.33)

K6=(5000*.02)/(5000*612)

K7= (700*.22*.01)/(700*4740*.33)

```
K8=((700*.22*.01)/700)

K9=(5000*.02*.01)/(5000*612)

K10=((5000*.02*.01)/5000)

K11=.00904

K12=.0168
```

REM TRIGGERFISH VALUES assume 4% of body weight removed & 8% net growth

REM BIOMASS IS 70 KG/HA

REM ASSUMES URCHINS 1% OF MAXIMUM WHEN TRIGGERFISH ABUNDANT

```
K13=((70*.04)/(70*5000*.01))

K14=(70*.04*.01)/(70*5000*.01)

K17=((70*.04*.01)/70)

K19=(70*.04*.01)/(70*4.93)

k20=(49.3-4.93)/(70*4.93)
```

REM fishing coefficients

```
K16=.04

k18=.04
```

REM PISCIVORES 25 KG/HA EAT 4% OF BODY WEIGHT AND 1% TURNOVER AT MAX. BIOMASS

REM HERBIVORES FISH 700 KG/HA WHEN PISCIVORES ABUNDANT

```
k21=(25*.04)/(500*25)

k22=(25*.04*.01)/(500*25)

k23=(25*.04*.01)/25
```

REM coral loss due to spine abrasion

```
k25=.0001

startrun:
```

```
ins=43835!
a=1000
ra=49.3
sa=3528
h=1528030!
c=1000
  u=100
  t=70
  f=500
  p=25
REM cm is the constant for converting mass to height where
3682=kg/head  &  hha=heads/ha
  hha=415
  cm=hha*3682
 x=0
  T0=25
sfast=10
swpar=100^sfast
nd=7:z2=dt/2:z6=dt/6
x(1)=a:x(2)=c:x(3)=u:x(4)=f:x(5)=t:x(6)=p:x(7)=h
a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)
starttime:
330  PSET  (x/T0+10,yone-a/200)
340  PSET  (x/T0+10, yone-c/200)
360  PSET  (x/T0+10, ytwo-u/100)
370  PSET  (x/T0+10, ytwo-f/20)
375  PSET  (x/T0+10, ythree-t/4)
```

```
380  PSET  (x/T0+10, ythree-p/5)

390  PSET  (x/T0+10, ysize- h/40000!)

TME=x/365

LOCATE 15,17: PRINT "time, a, c, f, p, t, u, h:": PRINT USING "######.#
"; TME; a; c; f; p; t; u; h

LOCATE 17, 15: PRINT "ac, be:": PRINT USING "####.#"; ac; be

 GOSUB model

 FOR I = 1 TO nd:Z1(I) = d(I):Z7(I) = x(I):z2(I) = x(I) + Z1(I) * z2:x(I) =
z2(I): NEXT

 tim= Z9 + z2

 GOSUB model

 FOR I = 1 TO nd:Z3(I) = d(I):Z4(I) = Z7(I) + Z3(I) * z2:x(I) = Z4(I): NEXT

 GOSUB model

 FOR I = 1 TO nd:Z5(I) = d(I):z6(I) = Z7(I) + Z5(I) * dt:x(I) = z6(I): NEXT

 tim= Z9 + dt

 GOSUB model

 FOR I = 1 TO nd:x(I) = Z7(I) + (Z1(I) + 2 * Z3(I) + 2 * Z5(I) + d(I)) * z6:
NEXT

 a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)

 x=x+dt

IF x/T0<xsize-10 THEN GOTO starttime

PRINT #1, USING "########.### ";  TME; a; c; f; p; t; u; h; ca

m=m+.015

IF m< .12 THEN GOTO startrun

CLOSE #1

STOP

REM MODEL GOES HERE
```

model:

a=x(1):c=x(2):u=x(3):f=x(4):t=x(5):p=x(6):h=x(7)

u3=u^sfast

sw=u3/(swpar+u3)

REM CALCULATING

RI=ins/(1+a*sa*K0)

RF=RI/(1+c*sa*K00)

jr=ra/(1+t*k20*(1-sw))

height=h/cm

sa=(3.596+6.723*height)*hha

d(1)=a*RI*sa*K-a*K1-a*f*K5-a*u*K6

d(2)=c*RF*sa*K2-c*K3-c*u*k25

d(3)=u*a*K9-u*K10-t*u*K13*sw

d(4)=f*a*K7-f*K8-p*f*k21-M*f*K16

d(5)=t*u*kl4*sw+t*jr*K19*(1-sw)-t*K17-t*M*k18

d(6)= p*f*k22-p*k23-M*p*k18

ac=c*k4+a*k24

be=f*k11+u*k12

d(7)= ac-be

CA=(M*f*K16+M*t*k18+M*p*k18)*365

RETURN

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BIOGRAPHICAL SKETCH

Timothy Rice McClanahan was born November 6, 1957, in New Haven, Connecticut. He lived in Minnesota, Connecticut, France and California before attending college. He received his bachelor's degree in biology from the University of California at Santa Cruz in 1981. He spent one year as an exchange student at the University of Nairobi, Kenya, in the Zoology Department and worked for the Kenyan Ministry of Natural Resources. He met his wife-to-be, Nyawira A. Muthiga, in Nairobi in 1978. In 1984 he completed an M.S. at the University of Florida, Environmental Engineering Sciences, Systems Ecology Program, focusing on revegetation of phosphate mined land. In 1984 he returned to Kenya where he taught at the international private college Friends World College in Machakos, Kenya, for 4 years. During this time he initiated the Coral Reef Conservation Project to study the impacts of fishing on Kenyan coral reefs. He was married to Nyawira Muthiga in January 1986 and had a son Robert M. McClanahan in March 1987. He returned to the University of Florida in January 1988 to complete his doctoral degree on Kenyan coral reefs in the Department of Environmental Engineering Sciences, Systems Ecology Program.
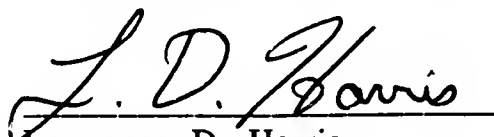
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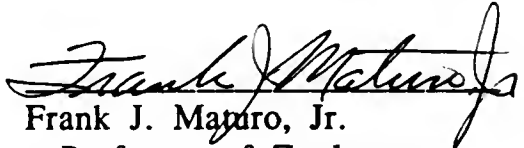Associate Professor of
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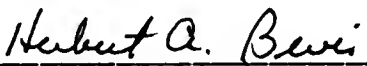
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